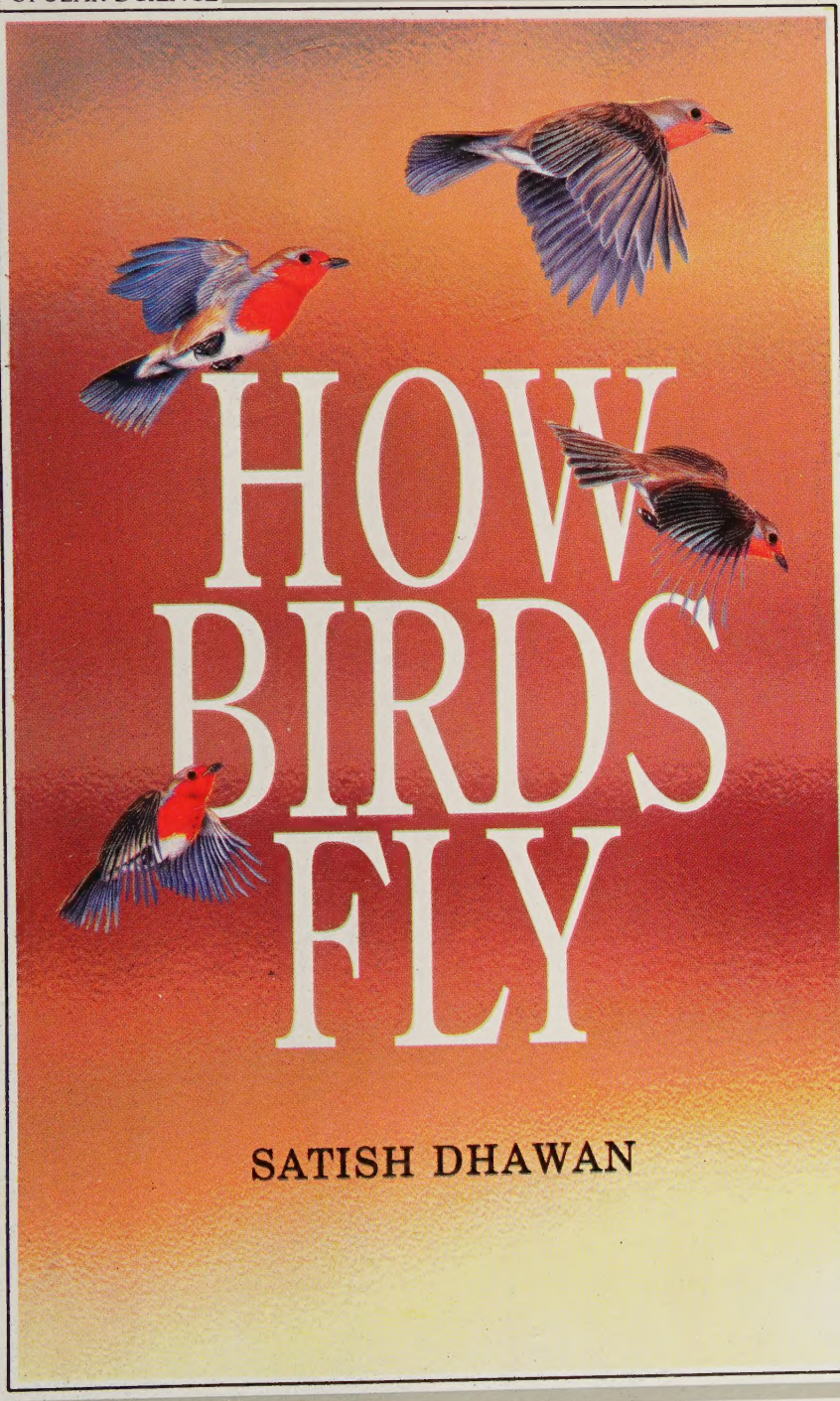
POPULAR SCIENCE



HOW BIRDS FLY

SATISH DHAWAN

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How Birds Fly

Popular Science

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SATISH DHAWAN

NATIONAL BOOK TRUST, INDIA

ISBN 81-237-3738-6

First Edition 2002 (*Saka* 1923)

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Rs 40.00

Published by the Director, National Book Trust, India
A-5 Green Park, New Delhi-110016

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Foreword

It is very thoughtful of NBT to bring out a popular version of the special publication of *Bird Flight*, authored by Prof. S. Dhawan, that first came in print in October 1990. The original publication brought out by the National Aeronautical Laboratory of Council for Scientific and Industrial Research (CSIR) was based on the CSIR Raman Memorial Lectures delivered by Prof. Dhawan. Even after more than a decade, the topic chosen by Prof. Dhawan continues to fascinate us all. This popular version is therefore bound to satisfy the curiosity of a large number of students and members of the public who look at science with a sense of adventure and wonder.

I am indeed honoured to have been requested by NBT to write a Foreword for this new version of *Bird Flight*. I recollect with nostalgia the day— 11 February 1991 to be precise—when Prof. Dhawan handed me a personal complimentary copy of his original book, with his usual humility when he wrote in his hand, *'Herewith a copy for you. I've found a few misprints and errors; you can have fun discovering them yourself.'* With that challenge I did manage to find some of them, but more importantly, I learnt a lot about this fascinating subject and more about Prof. Dhawan's interests as a naturalist and about his meticulous study as an engineer.

His respect and admiration for C.V. Raman as a genius, who had wide-ranging and deep interest in the investigation of natural phenomena, inspired and committed him to choose this topic and dwell on it with simplicity of a

naturalist and meticulous details of an engineer. He has challenged the scientific community to follow in the footsteps of Salim Ali, whose remarkable ornithology studies left a memorable imprint on this doyen of the Indian space programme. Prof. Dhawan's dedication as well as professional and managerial skill, that one sees in this book, has taken the Indian space programme to soaring heights beyond the flights of birds.

The present edition of *How Birds Fly* has retained the original simplicity of the topic, elaborated and explained with the help of several drawings and photographs, without demanding from the reader a knowledge of the complex mathematical equations that the author had originally included in his technical presentation to professionals. Simple answers to the various questions that come to your mind when you observe the flight of a bird are still available in this popular version of the book. To that effect the value of the book has been enhanced in that it has been made accessible to a much wider community who care to think and wonder about natural phenomena.

At a time when young students are moving away from science as a subject for higher studies, it is important that this book catches the attention of the large number of students and their parents. I hope that NBT, with its expertise in conveying knowledge to a vast population of its readers in the rural areas through regional and local languages, will make special efforts to ensure a wider circulation of this book, and promote the development of a scientific temper among the people of India.

It is sad that Prof. Satish Dhawan, who passed away on 3 January 2002, could not see his work in this form. I am sure he would have been delighted to personally hand over copies of this book to the large number of young students whose curiosity fascinated him.

Bangalore
14 January, 2002

P. J. LAVAKARE

Preface

C.V. Raman was a genius with extraordinary, wide ranging and deep interest in the investigation of natural phenomena. His exuberant delight in communicating the beauty and excitement that he found in science inspired a whole generation. It is an honour and privilege for me to be invited to give the CSIR Raman Memorial Lectures during the Raman Centenary Year. I chose to speak on bird fight as the subject had intrigued me for many years and I had first lectured on the subject to the Indian Academy of Sciences at its Annual Meeting in 1978 at Hyderabad. I also felt that the topic, spanning the physical and biological sciences, could be of interest to a wider audience in India where, apart from Salim Ali's remarkable ornithology studies, there has been little research on the flight aspects. Since the day of the pioneers of mechanical flight, almost a hundred years ago, scientists from many fields and lands — fluid dynamics, and aeronautical engineers, physicists and biophysicists, physiologists and zoologists, engineers and applied mathematicians, have studied animal locomotion of which bird flight is a special and unique case.

I find it surprising that the subject seems to have attracted no active scientists in India. I was fortunate, during my association with the Indian Space Research Organisation, in being able to use the high speed rocket

flight photography facilities at the SHAR National Space Launching Range. With the adjoining Pulicat lake, Nelapetu and other bird sanctuaries providing excellent opportunities for observations on a variety of birds, I requested a colleague to help me with high speed photography. These lectures attempt to explain, in simple terms, the physical principles which underline bird flight. I lay little claim to originality and acknowledge my debt to the many distinguished researchers on animal flight who have made the subject a new branch of science. I am no less indebted to the birds, especially those whose flight is recorded in the films and photographs.

The lectures were delivered at the CSIR Laboratories in Jammu and Jorhat and at the University of Cochin, Cochin to rather diverse audiences composed of scientists, students as well as lay persons. The core of the lectures was around a set of high speed films of eleven birds — kingfisher, sparrow, egret, kite, tern, pigeon, ibis, crow, painted stork, pelican and a vulture — showing their flight in slow motion. Not unexpectedly, each lecture turned out to be somewhat different from the other. In order to provide the reader a flavour of the dynamics of bird flight, a few sequential photographs from the films have been included as a flip strip, starting from p. 21. I regret that due to other demands on my time I could not write up the lecture material sooner; the extra time has however allowed me to include results of more recent research, especially on the muscular power available.

Finally, I express the hope that at least some readers would find enough interest to venture beyond the boundaries of their own specialisations and contribute to this fascinating subject.

Bangalore
March 1990

S DHAWAN

Acknowledgements

I am grateful to Dr A.P. Mitra, Director-General, CSIR, for the invitation to give these lectures. The Director and staff of RRL, Jammu and RRL, Jorhat, the Vice-Chancellor, University of Cochin and scientists from National Institute of Oceanography, Goa made all the arrangements for my stay and provided the projector and other facilities for the text. My former colleague in ISRO gave me unstinting support in obtaining reference material, in the reproduction of photographs, etc. I thank Dr S.K. Sinha and Dr K.S. Prabhu for help with some of the numerical computations. Mr K.R. Seetharaman, scientist at SHAR Range, was responsible for all the high speed bird photography and the films, and I thank the Director, SHAR and his colleagues for the facilities they provided me. The librarians and staff of ISRO headquarter, Indian Institute of Science and National Aeronautical Laboratory were most helpful in locating and loaning reference material. The help from ISRO technical liaison unit, Washington is acknowledged in obtaining copies of some important references. The arduous and taxing work of typing, editing, reprography and formating has been most ably and cheerfully done by my secretary, J.R. Kasturi. Prof R. Narasimha and Shri Shyam Chetty of NAL were very kind to help me in many ways. I thank Dr S. Bhogle and his colleagues of the Information Services Section at NAL for their effort in bringing out the material in its final form.

1

INTRODUCTION

Since times immemorial man has been fascinated and intrigued by the beauty, grace and intricacies of bird flight. There is perfect harmony of form and function. It is equally exhilarating to attempt to understand how the physiology and performance of birds are related to scientific principles.

Birds evolved from reptilian stock during the Jurassic period some 150 million years ago. Insects were the first life form to conquer the air earlier, during the Carboniferous period, about 300 million years ago. The pterosaurs also preceded the birds. These flying animals had evolved wings in which a membrane or skin was stretched out between elongated fingers. Until recently it was generally considered that Pterandon, with a wing span of about 7 metres and weighing 16 kg was the largest flying animal that inhabited the earth. However, in 1971, the skeletons of a pterosaur — *Quetzalcoatlus Northropi* (Q.N.), were discovered in Texas, USA. It has been deduced that Q.N. had a wing span of 11 metres and weighed about 64 kg. By the late Cretaceous period the flying reptile experiment seems to have failed and the pterosaurs were extinct. The evolution of birds overlapped the pterosaurs but is considered quite distinct from them; in fact, the two flying forms must have been in competition for the same ecological niche with the birds eventually proving spectacularly more successful.

Evolution

While there are several theories regarding the lines of bird evolution, it is generally accepted that birds evolved from reptiles and have come from the same stock as dinosaurs. Two main theses have been advanced about the route followed. One suggestion — the 'cursorial' theory — is that the ancestor was a bipedal ground-dwelling reptile which, whilst running rapidly, derived advantage of aerodynamic lift from its forelimbs. Another view is that the first birds were arboreal in habit and had evolved from tree-climbing, lizard-like reptiles who used their forelimbs in gliding from tree to tree. Evolutionary advancement must have led to the scales on the forelimbs becoming elongated, eventually developing into feathers. Very little is known about the detailed process of evolution and it is possible that during the transformation of scales into feathers, there was need for body temperature control and the aerodynamic advantages which accrued were really fortuitous. Obviously a stage was eventually reached when the aerodynamic qualities increasingly gave decisive advantages. The freedom of movement, increased access to new food supplies and a more efficient means of escape from enemies and predators — these factors must have become the prime foci for evolutionary change. The oldest fossil remains discovered, which display all the essential characteristics of a bird, are those of Archeopteryx found in limestone rocks in Bavaria, West Germany in 1861, two years after the publication of Darwin's *Origin of Species*. It was probably a poor flier compared to the birds of today. Its wing claws helped it to clamber about in trees and perhaps by flapping its wings it could move from tree-top to tree-top — often gliding part of the way. Fossils of birds since Archeopteryx have also been found. Two of them, the Ichthyornis and the Hesperornis, are shown in Fig. 1.

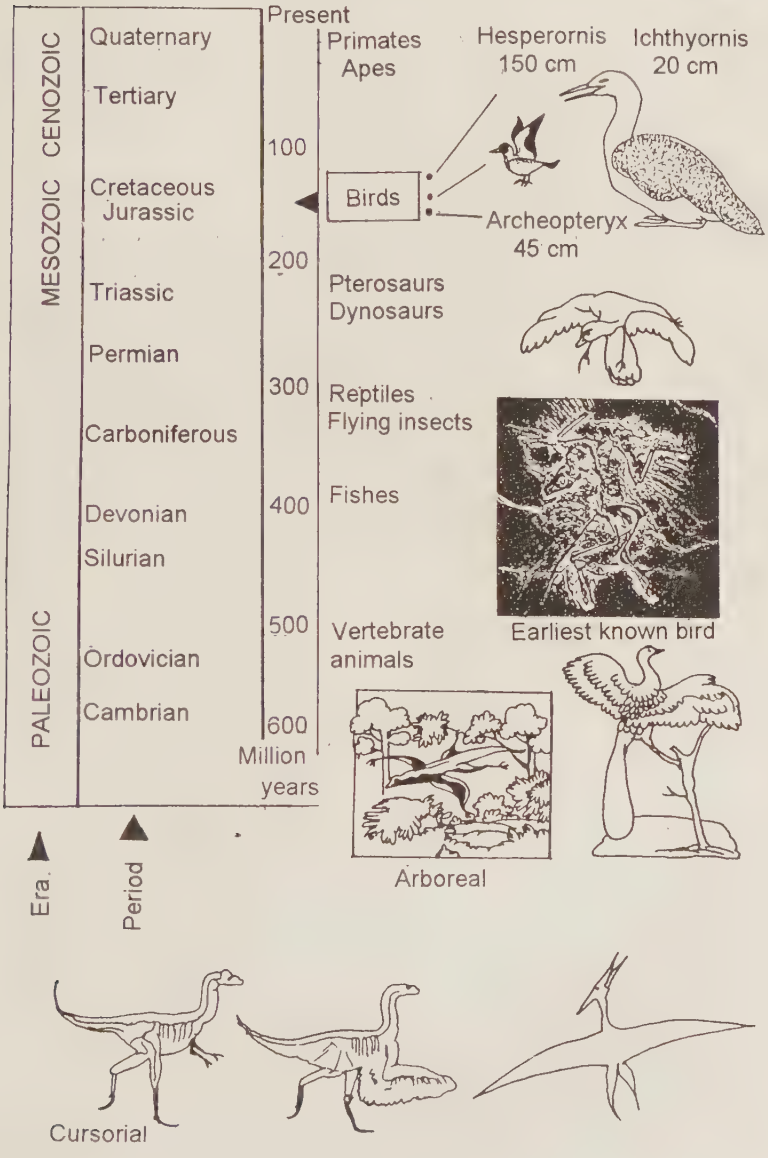


Fig. 1: Dinosaur to bird.

Both became extinct long ago. Other more recent extinctions are the Dodo and the great Auk which were extant only a few hundred years ago.

Species

Today birds inhabit every continent. There are nearly 9,000 species classified into 27 orders. Some orders have only one species. The order Passeriformes (perching birds) contains the largest number of species (70). It is generally been found that the survival rate of the primitive orders is much poorer compared to the highly evolved ones.

James Fisher, the ornithologist, has estimated that the world population of birds is approximately 100 billion. The most abundant are the oceanic birds of the large land masses. The distribution is roughly as follows:

South America	3,000 species
Africa	1,500 species
Indian subcontinent	1,200 species
China and Japan	1,100 species
North America and Canada	750 species
Russia	700 species
Australia	650 species

As noted before, the most highly evolved birds are in the Passeriformes order — sparrows, finches, crows, jays, etc.

The ability to fly — like many other biological properties of living things — came about as an adaptation to particular conditions. The variety of habitats and the varied responses to them has led to an incredible diversity of flight techniques and apparatus:

- Swifts spend most of their lives in the air.
- Sparrows cannot glide.
- The larger vultures are champion gliders but cannot take-off without a run into the wind.

- Penguins and ostriches cannot fly.
- Geese fly over the Himalayas (9,000 metres).
- The humming bird can hover for long periods.
- Arctic terns migrate between the Arctic and Antarctic continents — 18,000 km each way.

It would therefore appear as if no two species fly exactly in the same manner!

Pioneers of Flight

In this book we will examine some general features of bird flight — the flight apparatus of the bird and the modalities of flight. Man learnt to build aircraft machines — which enabled him to fly by studying birds. Pioneers like Otto Lilienthal (1849-1896) in Germany and E.J. Marey (1830-1904) in France and George Cayley (1773-1857) in England were among the earliest scientists who not only observed birds, but analysed their flying. Marey was among the first to realise that birds in flight could be properly studied only through high speed photography (Fig. 2a). More modern work by R.H.J. Brown, C.J. Pennycuick and V.A. Tucker has helped clarify the essential aerodynamics.

The Wright Brothers' first flight in a heavier-than-air machine (Fig. 2b) in December 1903 ushered mankind into the era of the conquest of the air. The science of flight — aerodynamics and flight mechanics—rapidly grew out of the earlier foundations laid by Newton, d'Alembert, Helmholtz, Rayleigh, Prandtl and Von Karman. The modern science of aeronautics is a very sophisticated combination of mathematical theory and physical principles supplemented by experimental measurements. Man has learnt to build aircraft which can carry 350 passengers 10,000 km non-stop across oceans, fly faster than a bullet and zoom

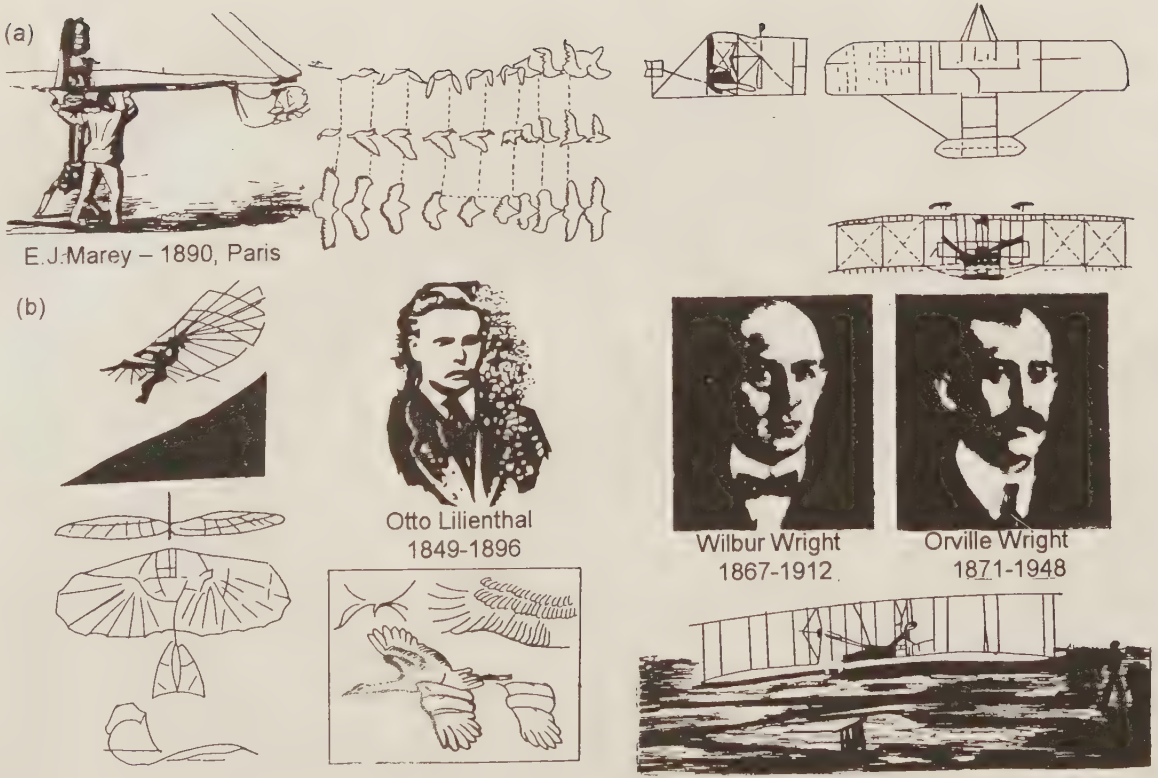


Fig. 2a & b: Pioneers of flight.

to the outer edges of the atmosphere, etc. and yet there are complexities of bird flight for which there is as yet no complete mathematical description. Man-made flying machines still cannot perform the range of manoeuvres that a blackbird or a sparrow can. There is still much which science can learn from the birds.

2

WHAT IT TAKES TO FLY

Among the living animal species, true flight is confined to insects, birds and bats. Man has to use machines to be able to fly. Before we examine 'how' a bird flies let us take a look at the essential elements necessary for flight. These are:

- A light-weight, high-strength structure.
- Wings and feathers for generating lift and forward thrust.
- The flight muscles which provide the power.
- A fast-response flight control and navigation system.

Adapted for Flight

The skeletal structure of the bird has evolved into an efficient light-weight structure consisting of the body-box— the rigid ribcage — with the many-vertebraed neck and tail remaining flexible. Essentially the skeleton is a frame for the attachment of the movable wings and the powerful flight muscles to the deeply keeled breastbone. The skeleton has evolved to suit the demands of walking and flying. Most of the larger bones are hollow and criss-crossed with supporting struts inside (Fig. 3).

Compared to reptiles or mammals, whose main mode of locomotion is on all fours, the bird's body evolution/ adaptation has caused a shift in the centre of gravity by a shortened body. The demands of flight have produced a

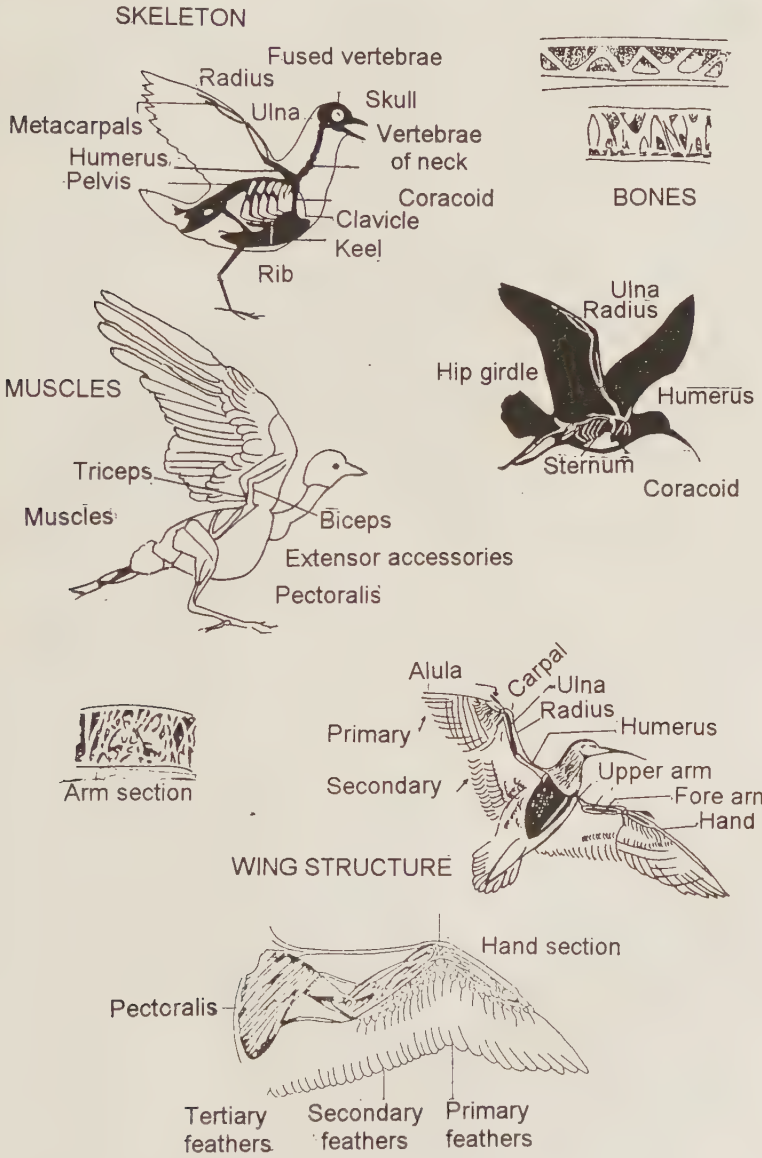


Fig. 3: Framework for flying.

relatively rigid, but a much lighter, skeleton.

The most remarkable features of the bird's flight structure are the wings and feathers. In the long evolutionary process, the forelimbs were transformed into wings. The bone structure of the bird wing is analogous to the human arm, wrist and fingers with obvious differences (Fig. 4). The upper arm, 'humerus', is proportionately shorter; the 'wrist' and 'palm' bones are fused together for greater strength in supporting the primary flight feathers. Of the three digits, 'fingers', two support the feathers. The third, 'alula', supports a small auxiliary wing extendable at will. This controls the airflow over the wing during landing and take-off manoeuvres — somewhat akin to a leading edge slot or flap on aircraft.

The bird wing is a complex flexible airfoil — cambered and adjustable for control. It tapers from root to tip and the planform varies with the type of bird, but generally has a characteristic shape. The feathers of a bird are perhaps their most unique possession and a marvel of engineering. A feather is both extremely light and structurally strong, yet very flexible. Feathers have greater strength/weight ratio than any man-made structure. Essentially a flexible structure, it is designed to be stiffer along the length than fore and aft. The shaft carries branches called *barbs* which in turn have off-shoots called *barbules* with the *barbicles* or hooklets which interlock like a zipper. The shaft or stem is hollow and filled with *keratin* — a horny substance of which the feather is made. Feathers are classified according to function:

- Primaries — usually 10 in the 'hand' — are unsymmetric, pointed and strongly arched.
- Secondaries — attached to the arm. Their number varies from bird to bird.
- Scapulars (shoulder feathers).

- Contour (external; determine outer aerodynamic shape).
- Down (insulation).

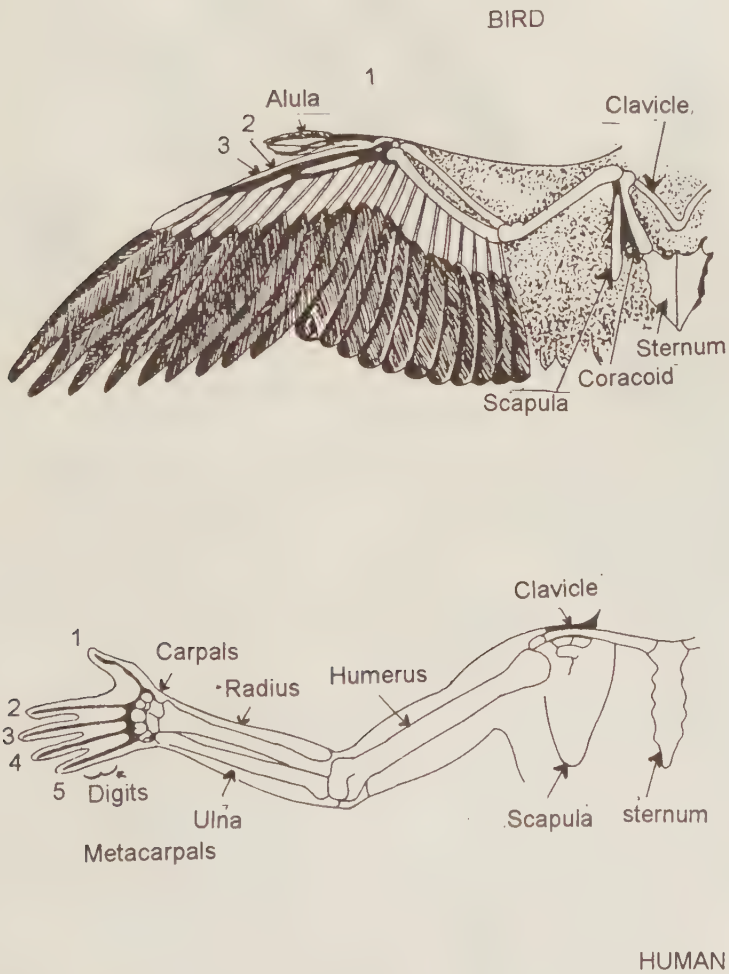


Fig. 4: Bird wing and human arm.

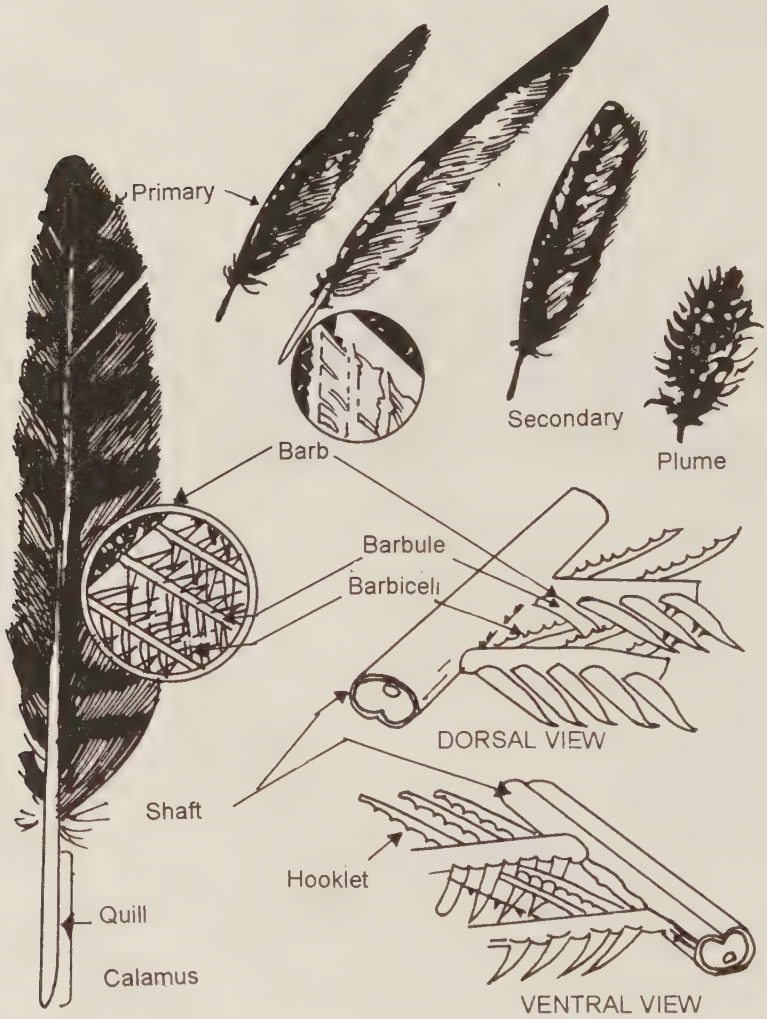


Fig. 5: Structures of feathers.

How many feathers does a bird have? There are approximately 1,000 feathers on a small bird! Typical examples are:

Gull	6,000
Duck	12,000
Swan	25,000

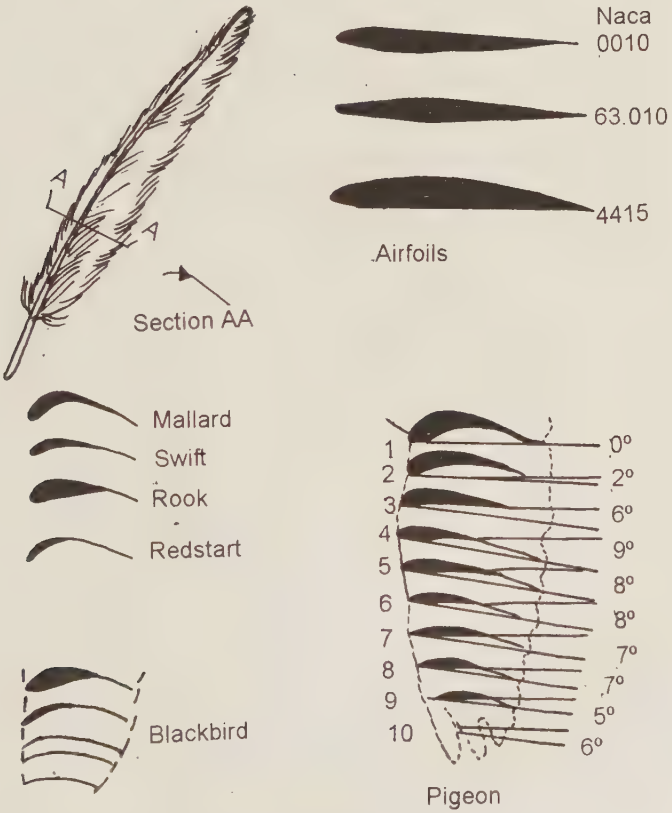


Fig. 6: Wing profiles.

A pigeon's primary feathers would have approximately 1,000 barbs and 500 barbules on each barb (Fig. 5). A complete feather may have about 10^6 (one million) barbules.

Feathers overlap, interweave and present a smooth, but not quite impervious, surface to the air. Each feather has an approximately streamlined profile. Along with the whole wing, a cross-section is generated which is aerodynamically similar to an airfoil section (Fig. 6). The profiles resemble, in a general way, those used for aircraft. An important point to note is that bird feathers and wings are very flexible; their shapes take on a range of variations depending on the conditions of flight.

The power for flight, through movement of the wings, is provided by two massive pectoralis muscles anchored to the deep keel of the sternum (Fig. 7). In the main power stroke (downwards), the large pectoral muscles contract to pull the wings down. Since muscles can work only through contraction, the return (or upstroke) is effected by a 'rope and pulley' system; as the pectoralis muscles relax the two 'supracoracoidus' muscles contract, raising the wing by means of a tendon running over the shoulder joint to the top of the upper arm. Since, during the upstroke, the wing movement is assisted by the air pressure, the secondary muscles are much smaller than the primary ones. The flight muscles may account for between 15-20 per cent of the total body weight. Considering the large variety of birds ranging in size from a few centimetres to several metres, and weighing from a few grams to several kilograms, the musculature can be expected to show significant variations in detail. Depending upon the dominant flight characteristics — fast flapping, slow flapping, soaring and gliding with occasional flapping, etc. the depressor and elevating muscles vary in size. Thus small

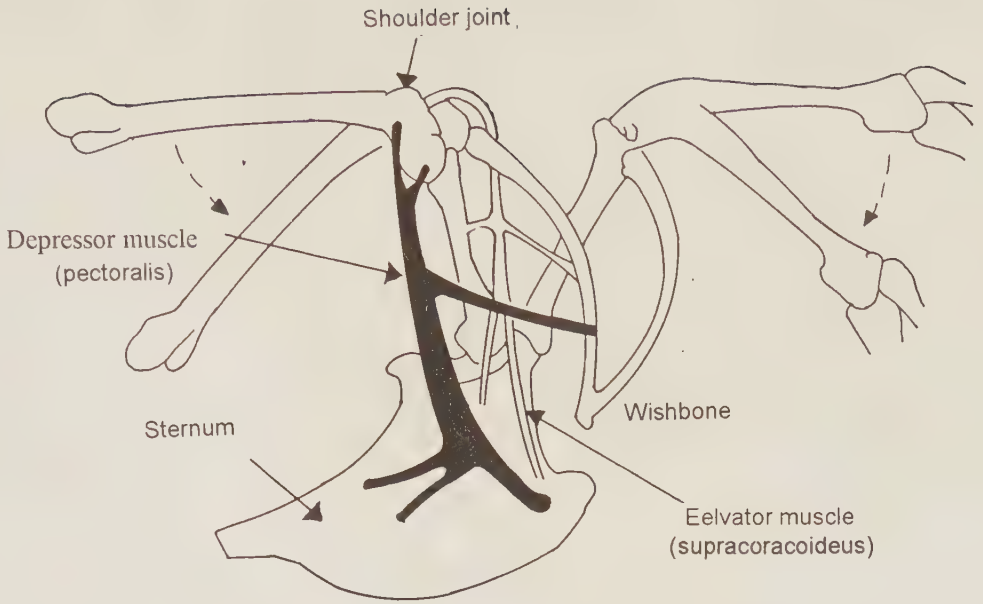


Fig. 7: Muscle action.

passerines have elevators much smaller than the depressors — so also the large, slow flapping birds. The structure varies depending on whether the muscles are to supply the necessary power continuously or intermittently. Humming birds have large elevators. So do medium-large birds which produce propulsion as well as lift on both down- and up-stroke. They have elevators not much smaller than the depressors. On the average, the small or secondary pectoral muscles are about 10 per cent in weight of the large pectoralis.

Flight Control and Navigation

All birds, in their search for food and avoidance of predators, have to manoeuvre in flight, i.e. change the direction of motion in a controlled manner. As flying machines, birds are inherently unstable and their flight is controlled and maintained by the neuro-muscular control of shape and position of the wings and tail. This instability appears to be a general feature of all animal mechanisms. Stability and manoeuvrability are inherently antagonistic qualities. A highly stable system is little affected by external disturbances or forces and would require relatively large forces to change its direction. An unstable system is easily upset but requires small control forces to correct the deviations and change the direction.

Birds are equipped with excellent eyesight — no other living being can match their visual acuity. Most birds are equipped with both monocular and binocular vision. Coupled with the sense of hearing, the birds' awareness of the external environment is accurate and fast. The fast sensory system is able to detect deviations during flight such as gusts, turbulence, etc. and also provide the assessment for avoidance of obstacles, etc. Control of pitching, rolling and yawing are accomplished by movement of the

tails and wings — sometimes differential changes, sometimes coordinated — as also through changes in the flapping modes of the wings, i.e. unequal beat frequencies and amplitudes.

Birds migrate over long distances. The question of navigation is still not resolved. It is known that some birds use sun orientation; others use the earth's magnetic field. However, the question is still not fully understood and will not be discussed in detail here.

3

TYPES OF BIRD FLIGHT

Before we take up a discussion of the way in which the bird's wings produce the required forces for flight, it is useful to take a general look at the main types into which bird flight may be classified. Although practically every species seems to have some specific features, it is easily observed that, broadly speaking, there are two main types:

- Flapping flight.
- Gliding flight.

Every bird flaps its wings in (what generally appears to be) an up and down repetitive fashion. Some birds flap continuously throughout their flight. Others may, after attaining adequate speed and altitude, stop the flapping motion and glide like sail planes on their outstretched wings — flapping again when required. Yet others may alternate between flapping and gliding — 'bounding' like some kingfishers and small birds.

Flapping Flight — 'Power-On'

Flapping flight can be regarded as 'power-on' flight since the bird continuously expends energy in flapping its wings and generates the thrust and lift forces to propel it and overcome gravity. Careful observation shows that, while the general manner of wing flapping motions may appear similar in all birds, there are many subtle differences

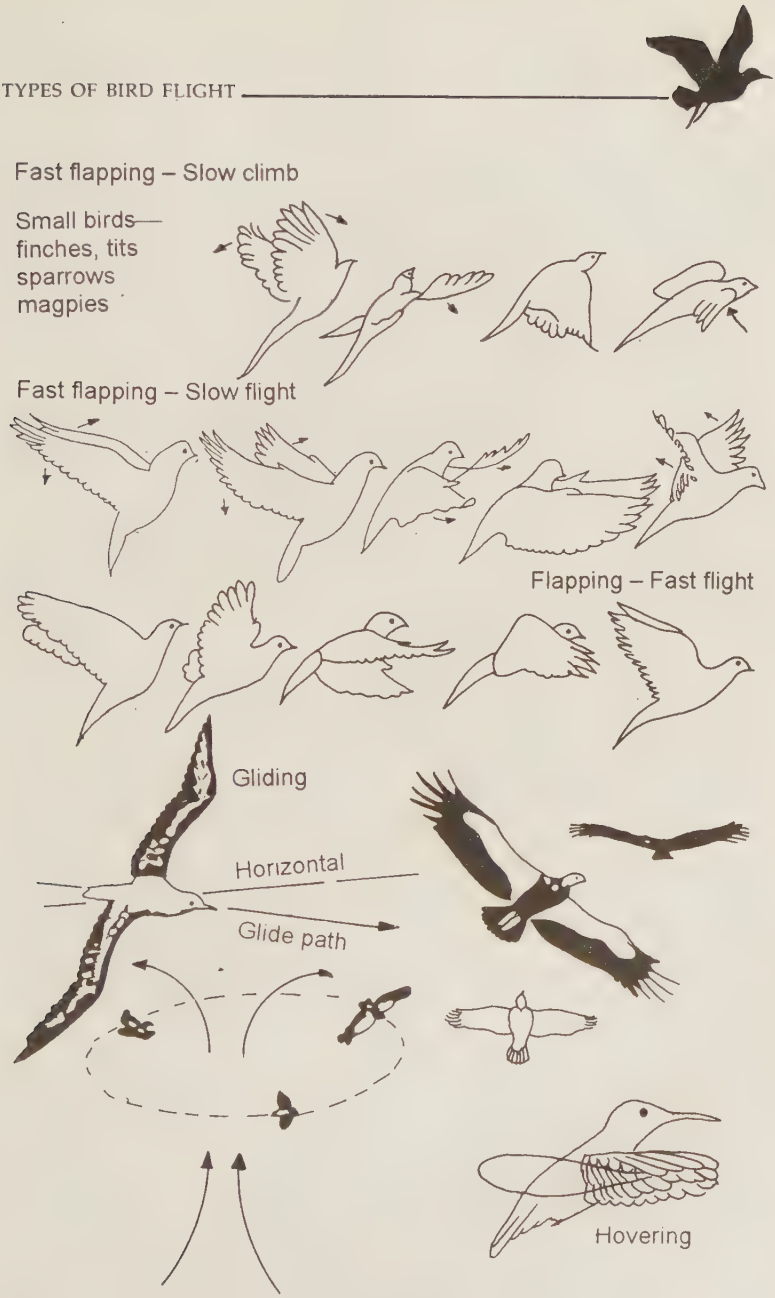


Fig. 8: Types of bird flight.

between the small and large birds (Fig. 8). The motion of the flexible wings is not only in the up and down direction but there are also forward and backward components, and parts of the wings twist during the flapping cycle. The actual wing configuration during the process of flapping can be studied in detail only with the help of high speed photography.

High speed photographs reproduced from various sources, serve to illustrate the complexities of wing form (Fig. 9) and attitude during flapping flight. Detailed studies show that the wings perform a dual function, working both as airfoils and propellers. Lift and propulsion are effected by a complex combination of vertical and horizontal motions along with bending and twisting of the wings during the flapping cycle.

Broadly speaking, the inner and outer parts of the wing perform distinct functions. The inner part, closer to the shoulder, with a lower amplitude of motion, also undergoes relatively smaller changes in attitude and mainly carries the lift during normal cruise flight. The outer wing — the hand section with the primary flight feathers — performs two roles. The first is as a propeller providing thrust and the second is to provide lift and control. The first function is common to all birds but the details of the second take on different forms, depending upon the size of the bird. During flapping flight one can distinguish two distinct movements of the wing. The first is the 'downstroke', or the power stroke, during which the wing generally moves downwards with the outer and faster moving part also moving forward, especially towards the end of the stroke. The second movement — 'upstroke' — essentially restores the wing to the fully up position from which the next downstroke starts. However, in the upstroke, so as not to produce unnecessary resistance (drag)

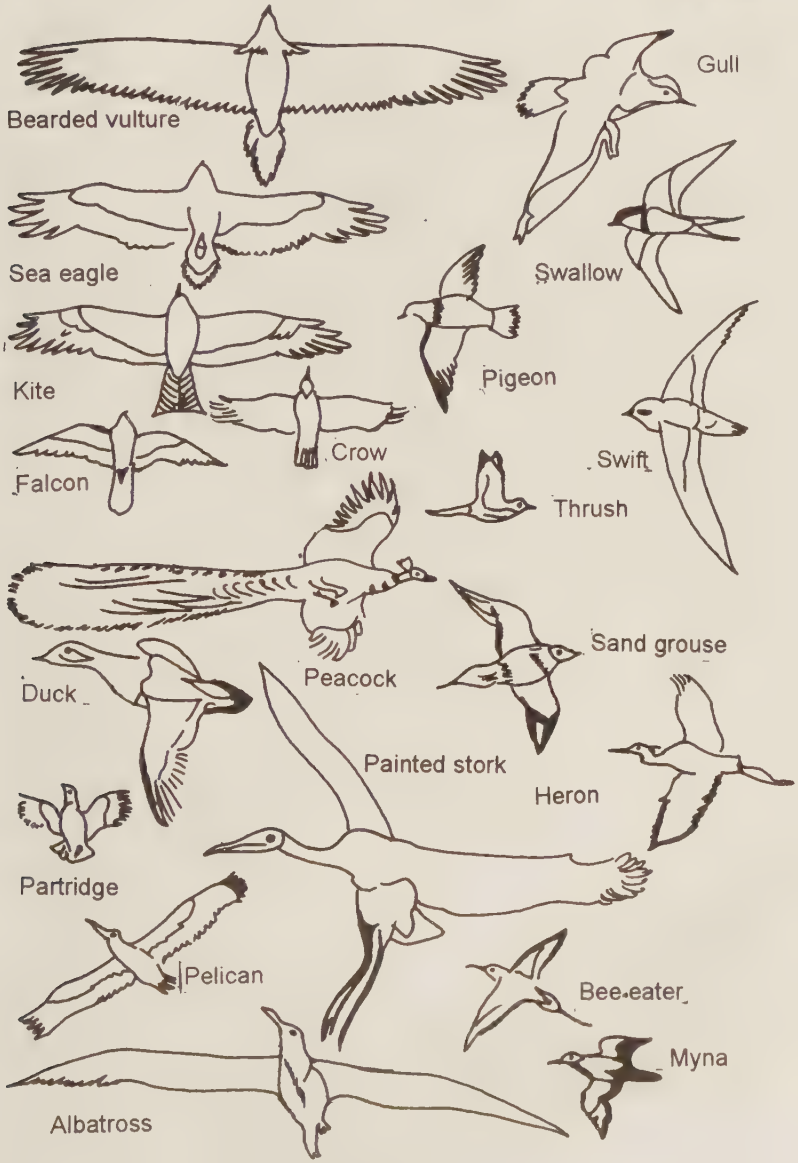


Fig. 9: Wing shapes.

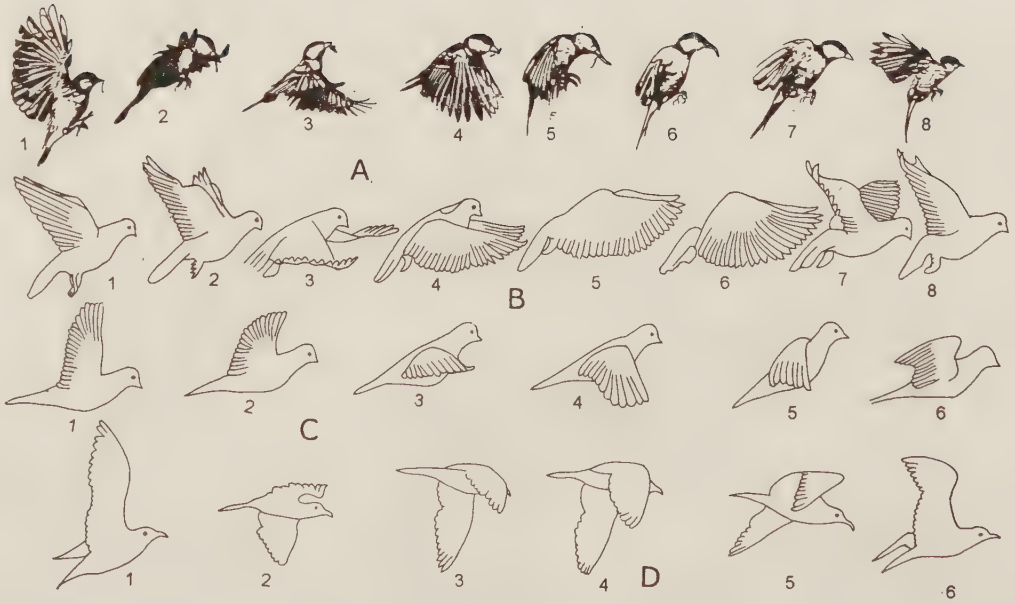


Fig. 10: Illustration of flapping flight of small (A), medium (B and C) and large (D) birds. A: great tit climbing (downstroke 1-3; upstroke 4-8); B: pigeon in slow flight (downstroke 1-4; upstroke 4-8); C: pigeon in fast flight (downstroke 1-4; upstroke 5-6); D: fast flight of a gull (downstroke 1-3; upstroke 4-6). Note the forward bending of primary feathers in A-3, B-3 and C-3 indicating lift+thrust; B-7 shows propulsive flick or upstroke.

and lose the lift, the wing goes through a complex bending and twisting motion. At the end of the downstroke, the wing first rotates upwards from the shoulder, while the elbow is relaxed, so that the outer wing bends down as well as rotates to present the least resistance to forward motion. Approximately half way through the upstroke the outer wing is moved up and back at a very rapid rate with outer feathers separated. This action not only reduces the drag but, in some birds, actually provides extra lift and forward thrust. During the power (down) stroke, the primary feathers are held close together to produce a near perfect airfoil for producing the maximum lift and thrust with minimum drag. In the smaller birds like sparrows, tits, etc., the outer part of the primary feathers gets separated on the upstroke and functions like slots, allowing air to pass through, thereby reducing drag. This does not occur on many of the larger birds, like gulls or on birds with slender wings, like swallows. These birds partially close the outer tips while flinging them back, thereby producing some thrust (Fig. 10).

The most detailed studies have been in the case of the pigeon, *Columba livia*. Immediately after take-off the requirement of adequate thrust and lift causes the birds to use a 'tip reversal' upstroke during which the primary feathers generate both weight support (lift) as well as propulsion (thrust). The downstroke in this phase of flight primarily generates lift except towards its end. When flying very slowly the secondary feather region (inner wing) is not moving fast enough to generate much useful aerodynamic forces. At higher speeds the pigeon modifies its upstroke, bringing the wing close to the body with the primary feathers rotated and separated so that they present the 'Venetian blind' appearance similar to small birds (Fig. 10.A4). As the pigeon's flight approaches the normal

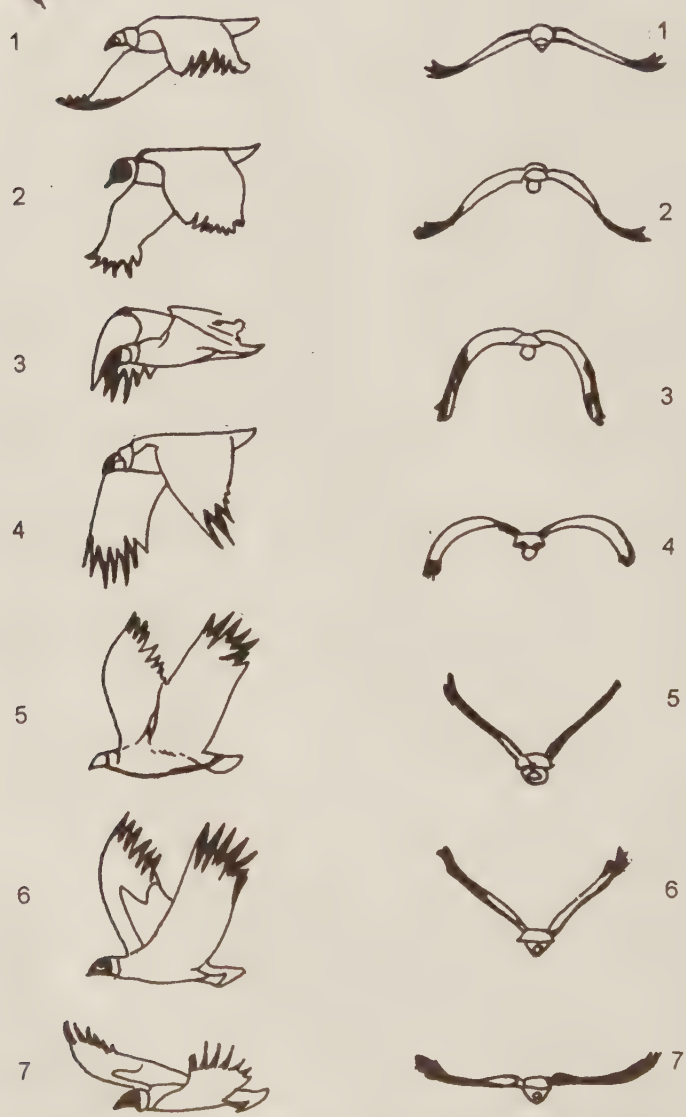


Fig. 11(a): Flapping of Andean condor. The angle of flapping is 40° up and 80° down (downstroke 1-3; wing flexes at wrist, midwing starts to rise 4; upstroke 5-7).

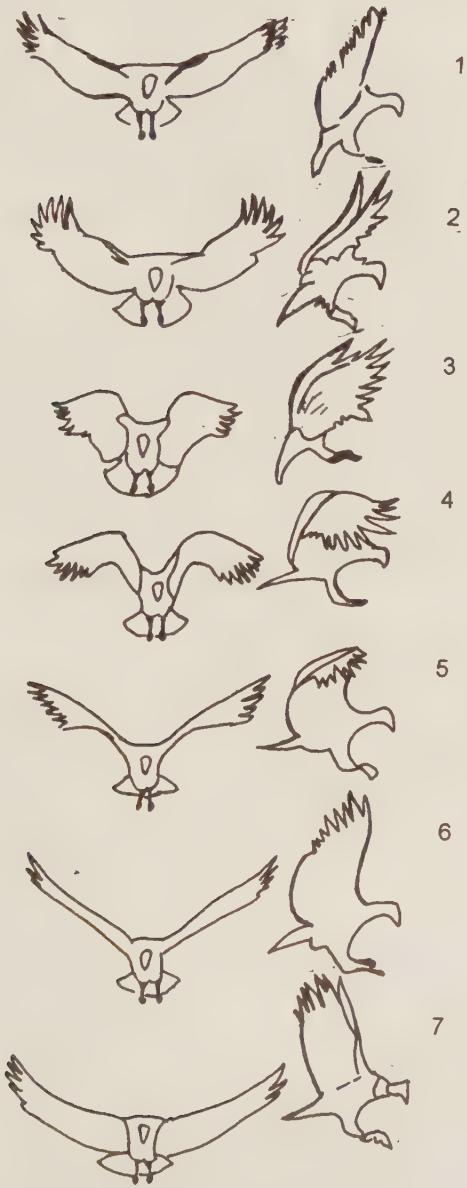


Fig. 11(b): Landing of Andean condor (downstroke 1-4; upstroke 5-7).

cruise speeds, the wing kinematics change again. Now the wings remain partially extended during the upstroke and force is generated throughout the stroke. Other birds, like the kestrel (*Falco tinnunculus*) also use this type of 'reduced span' upstroke in fast flight.

Take-off and Landing

During take-off, the forward speed of the bird being low, the primary requirement of lift to overcome gravity is essentially provided by a fast flapping rate which is higher than in normal forward flight (Fig. 11 a & b). The amplitude of flapping is also greater. Similarly, during landing, the speed being low, the bird's wings must generate the required lift to uphold the weight and also brake the forward motion. As a consequence, the wings are spread wide and the flapping motion adjusted (Fig. 12).

Propeller Action

Photographic observation of the flight phases shows that while a downward motion of the wings during flapping flight can be expected to generate lift, this, by itself, cannot propel the bird forward (Fig. 13). The 'propeller' function is performed by the outer and faster moving part of the wing through a change in attitude, i.e. twist, which moves the leading edge downwards as the wing moves forward. In this orientation the outer wings behave similar to the blades of a propeller. In fact, an observer viewing the bird from the front can easily imagine the flapping wings as equivalent parts of two contra-rotating propellers. The wing tips in their orientation and curvature clearly indicate the aerodynamic forces acting on them. It must, however, be noted that in each bird the precise orientation is not the same and, depending on the size and form, the functional kinematic aspects of wing flapping vary — only

Fig. 12: Take-off and landing of large birds. A: stork take-off (1-wing pulled forward on downstroke); B: owl upstroke after take-off; C: take-off of a large heron (1-downstroke beginning; 2-downstroke end with outer wing pulled forward and twisted); D: stork landing (1-steep glide with alulae raised and wings extended; 3-braking wing beats; 4-landing on rest).

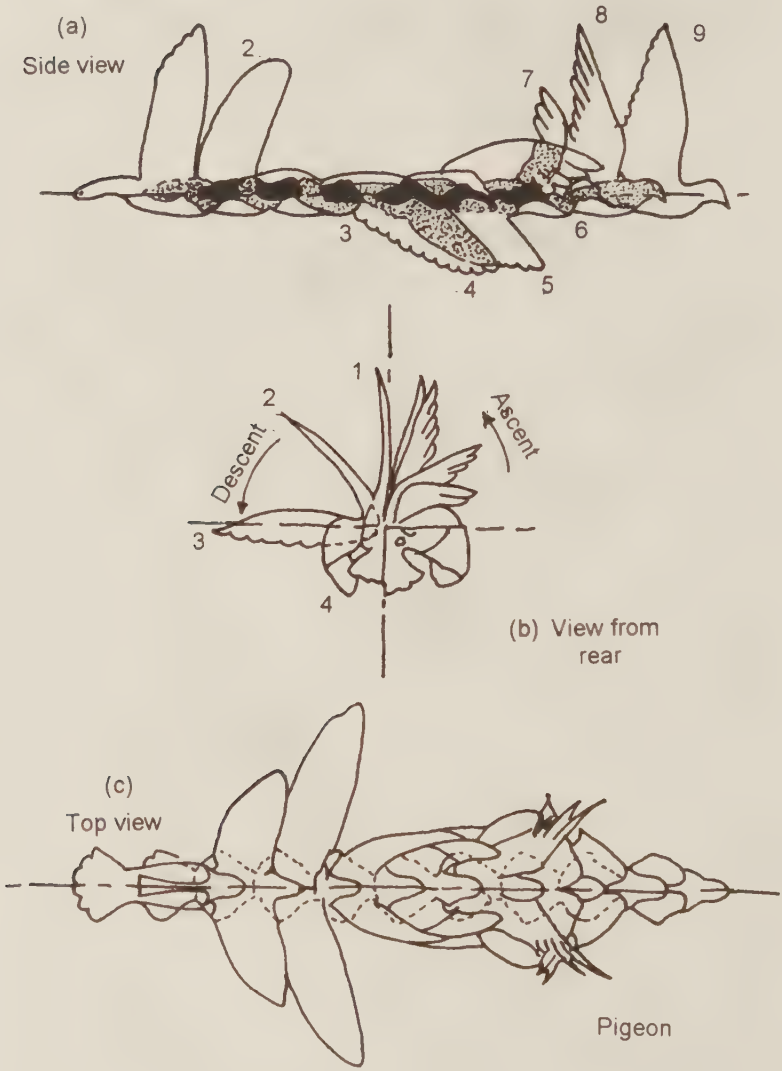


Fig. 13: Wing motions of pigeon in normal flight.

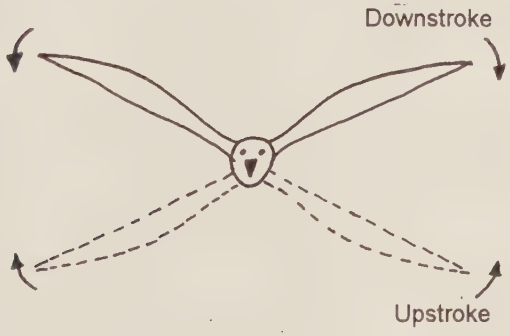
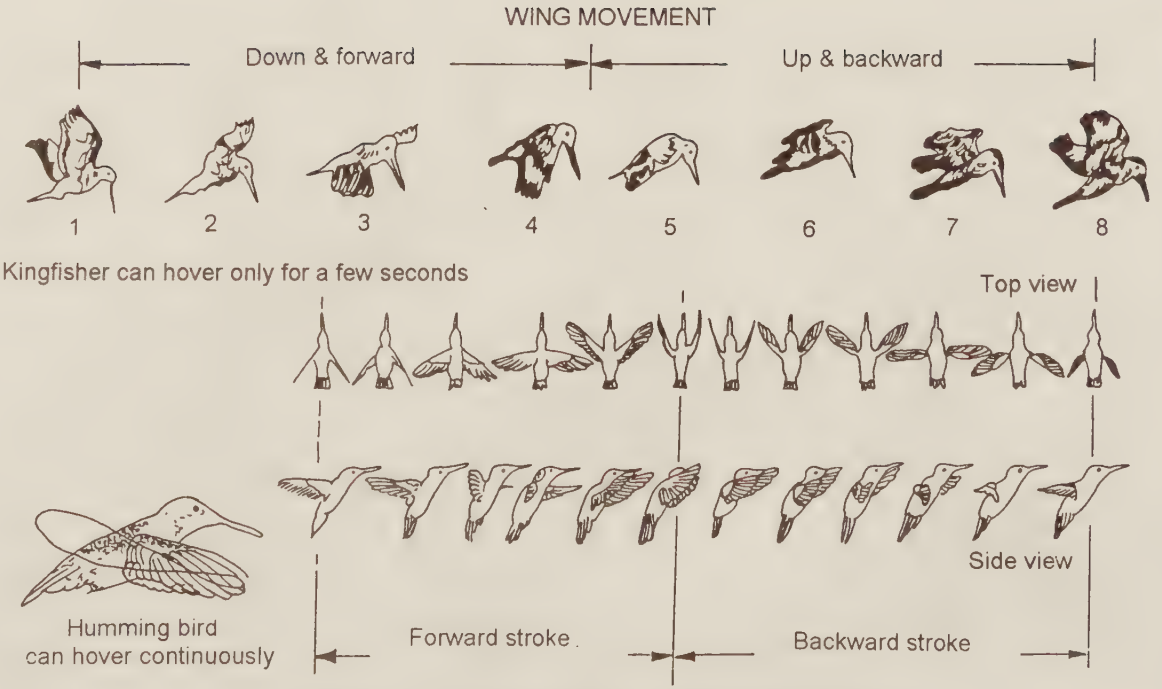


Fig. 14: Flapping wings as propellers.

confirming the complexities of flight (Fig. 14).

Hovering Flight

The ultimate in low speed flight, of course, occurs when the forward speed diminishes to zero, or practically zero, and yet the bird has to be airborne. The classic example of this type of flight is the humming bird of the American continent who hovers stationary in front of flowers while sipping the nectar. Other birds, such as sunbirds, are also capable of hovering for a short period of time — this is because of the extraordinarily heavy demands on energy that hovering entails. Only the humming birds are equipped with the musculature which will allow them to continuously hover. The kinematics of hovering flight demand wing movements such that, apart from a vertical reaction, forces are also generated in the horizontal plane. Fig. 15 shows how the humming bird accomplishes this in still air with forward and backward strokes during which the



Wings flap in a horizontal plane; bird remains stationary

Fig. 15: Hovering flight.

wing reverses its inclination. The flapping frequency is high compared to other birds — being between 50-100 hertz, depending on the size and weight of the humming bird (compared to 2-10 hertz for other birds in normal flight). Such hovering usually occurs in a prevailing wind current so that, relative to the bird, there is wind velocity and some lift available, while, relative to the observer, the slow forward motion of the bird is neutralised by the wind and the bird appears stationary. The wing flapping motion of the kingfisher shows that it has both up and down as well as back and forth motions. Similar hovering patterns can be observed in other birds, e.g. the kestrel as also smaller birds alighting or manoeuvring to catch insects. The humming bird also, in transitioning from hovering to forward flight, changes the flapping pattern of its wings so that an up-and-down motion appears in addition to the back and forth. This occurs alongwith a change in attitude of the body which is nearly vertical during hover and becomes horizontal during forward flight.

Gliding and Soaring

Gliding flight occurs when the bird does not flap its wings but uses gravity to provide the means for flight. In still air the path of the bird with wings spread is inclined downwards and the combination of the aerodynamic forces generated by the motion through the air and the force of gravity creates a balance of forces allowing steady gliding flight. Soaring takes place when a gliding bird is able to use air currents with vertical velocity components, such as thermals, slope currents near mountains, cliffs, etc. (Fig. 16). A particular form of soaring, known as *dynamic soaring*, can occur only when the wind has a velocity gradient with the speed increasing in the upward direction (i.e. away from the ground). The most familiar gliding

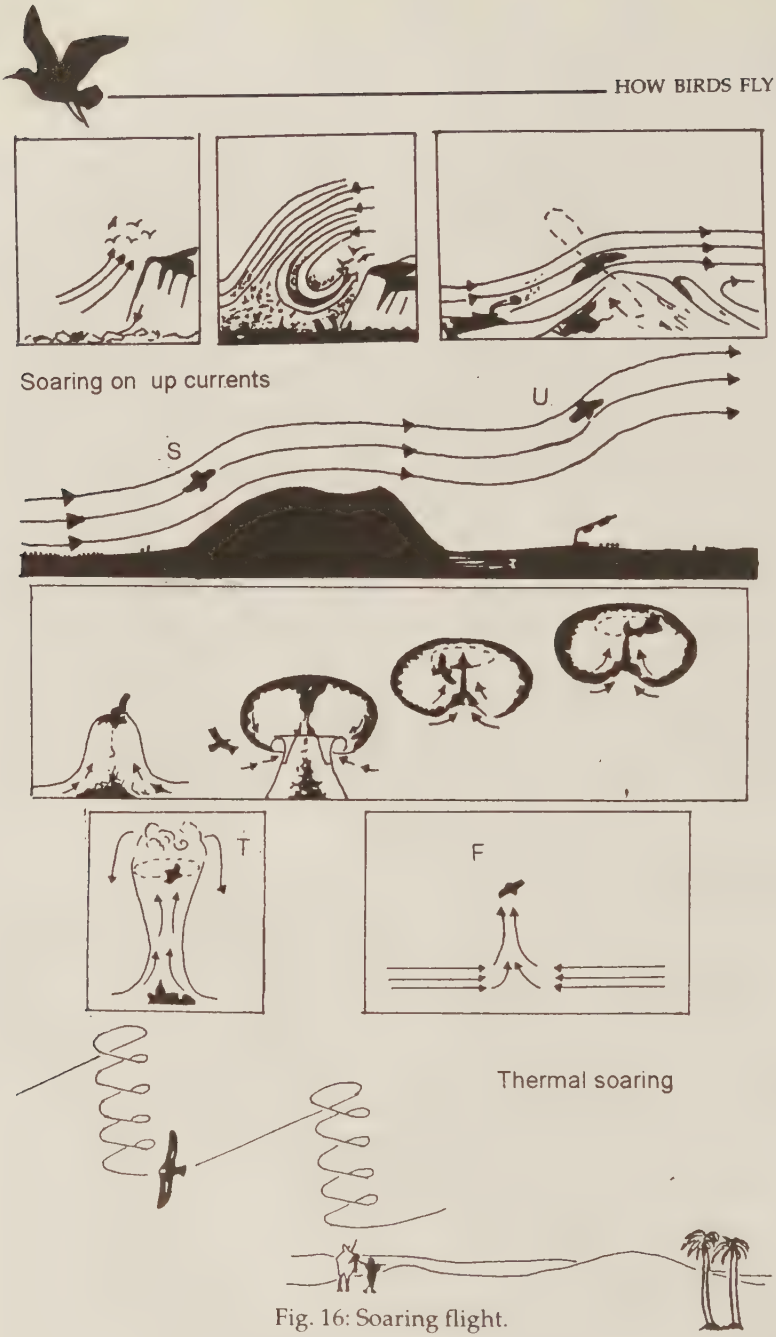


Fig. 16: Soaring flight.

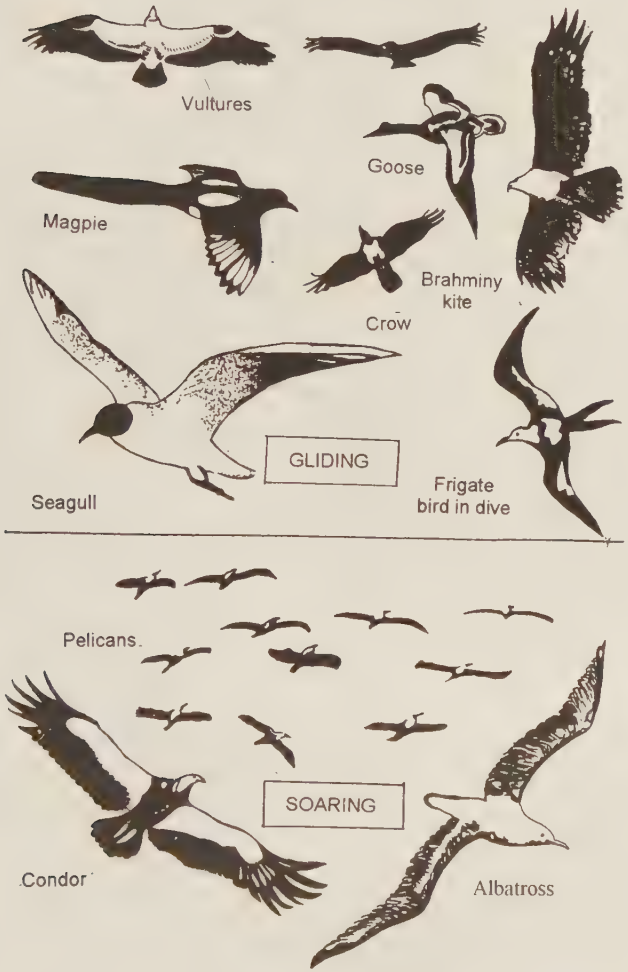


Fig. 17: Gliding and soaring.

and soaring birds are the vultures and kites. However, most birds — except the smallest — have the capability to glide and often use it during landing. It is interesting to recall that very careful observations of gliding and soaring birds were made by E.H. Hankin in India, in the early years of this century. Stationed in Agra, Hankin observed that birds of different weight and size followed soaring in succession after sunrise — the heavier ones coming later. He related this observation to the rising up-currents caused by differential heating of the atmosphere by the sun's rays. During gliding, while the bird expends virtually no muscle power, it does have to exercise some small movement of the wings for flight control and maintenance of stable flight. There are numerous birds other than the raptors which resort to periods of gliding (Fig. 17). Examples are sea birds like the gulls (*Laridae*), pelicans (*Pelicanidae*), crows (*Corvidae*), etc. As mentioned earlier, just before landing pigeons, pheasants, ducks, parrots and other smaller birds, such as the common mynas (*Sturindae*) and pheasants (*Phasianidae*) may go through a gliding phase.

4

WINGS FOR FLYING

In order to fly through the air a bird has to overcome gravity and generate a force which propels it forward. The science of aerodynamics and fluid mechanics seeks to understand and explain how forces arise on bodies moving immersed in a fluid (air, water). The foundations of the subject were laid in the last half of the 17th century when Newton enunciated the laws of motions of bodies. The development of aerodynamics has been a unique example of contributions by mathematicians on one hand and creative engineers, on the other. The names of Cayley (England), d'Alembert (France), Borda (France), Eiffel (France), Joukowski (Russia), Rankine and Reynolds (England), Prandtl (Germany), von Karman (Hungary) appear prominently among the scientists and engineers who developed the subject.

We rapidly recapitulate, in an elementary form, the manner in which lift and drag arise on a body moving through a fluid medium, such as air.

Flow Patterns and Forces on Airfoils

When a body — a bird or an aeroplane — moves through the atmosphere the air is disturbed. These disturbances take the form of minute pressure and density changes in the vicinity of the body. Depending on the size of the body, and its speed, they propagate to distances away from the

body up to a few body lengths. The scale of the atmosphere being large, compared to even the largest bird, the propagation distances are comparatively small. According to the principle due to Bernoulli, in a moving fluid the total energy is conserved. Thus in air flowing past a bird, the regions of higher velocity near the bird, caused by the disturbances created by the presence of the bird, would be regions of lower pressure and vice versa.

The simple case to consider is a circular cylinder moving with uniform speed through air. This is equivalent, by the principle of relative motion, to considering the cylinder being stationary and exposed to parallel uniform flow. If there were no viscous friction, the theory shows that there would be no net force acting on the cylinder. The air stream would divide symmetrically, around the cylinder — there being higher velocities at the top and bottom, and low speeds adjacent to the front and back faces. The associated pressure changes would be symmetrical; so no net force would act on the cylinder. Now if a clockwise circulatory motion is imposed around the cylinder, the velocity due to this motion will add to the earlier velocity field at each point. In particular, near the top of the cylinder, velocities would increase while, near the bottom, the velocities would diminish. The effect of these changes on the pressures would be to reduce the pressure on the upper surface and increase them on the lower one. Thus an upwards net force — the lift — would be created by the circulatory motion added to the streaming motion. It is clear that the greater the amount of circulatory motion, or 'circulation', greater would be the lift. When we deal with actual cases of wings and airfoils, whose shapes are not circular, the question arises: how much circulation would appear? Before we take up this issue, we must recognise the role of viscous friction (and the fact

Plate I: Migratory birds fly over great distances.

Plate II: A step by step picture of a white stork taking off and rising on warm soil.

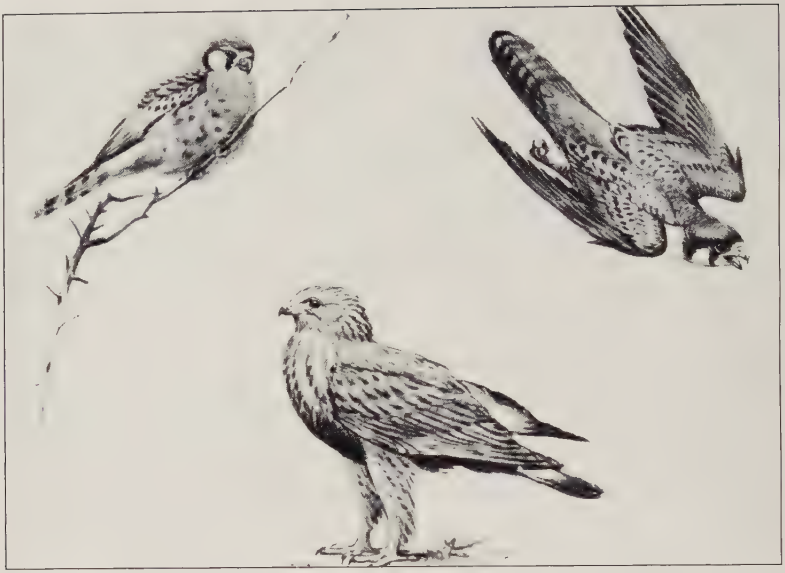


Plate III a: Shapes of wings of sparrow hawk, duck hawk and rough-legged hawk.

Plate III b: Swallow-tailed hawk, Cooper's hawk and caracara hawk.

Plate IV: The wings of a bald eagle.

Plate V: Some species of gulls that fly over water.

Plate VI: Geese often fly in V-formation on a long flight.

Plate VII: Arctic terns migrate over long distances by observing the position of the sun.

Plate VIII: A male warbler and a female warbler in mid-air.

Plate IX: The flycatcher's wings help it migrate long distances at night as well as day.

Plate X: This cutaway shows the aerofoil of a bird's wings.

Plate XI: The wing drops and the feathers dig into the air. This movement pulls the robin forward; then the feathers twist as the downstroke ends and the upstroke begins again.

Plate XII: The humming bird feeding on the nectar from flowers with its wings positioned to keep it in mid-air.

Plate XIII: A spotted harrier eagle has wide wings and flies slowly over open country.

Plate XIV: Note the position of the wings of this stork in flight.

Plate XV: These Japanese cranes, with wings outstretched, perform deep knee bends before stretching to full height.

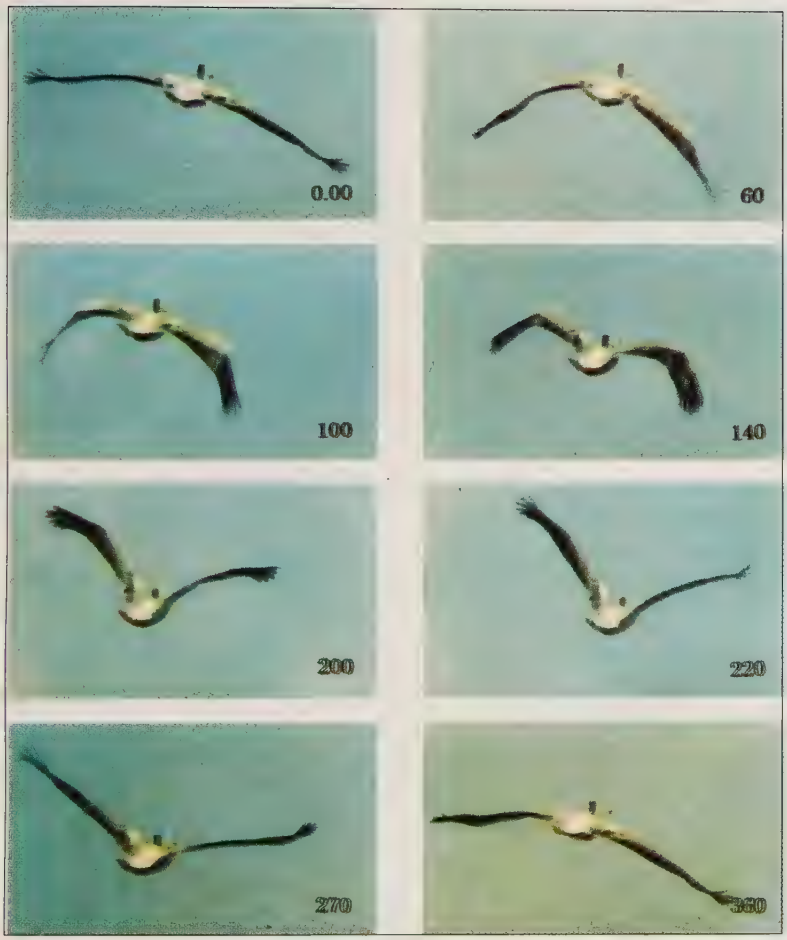


Plate XVI: Pelican in flight. Average flapping frequency: 2.5s. Framing rate: 100/s. Exposure: 500 µs. Lens: 300 mm, f-4.5. The number on each photograph indicates the time in milliseconds.

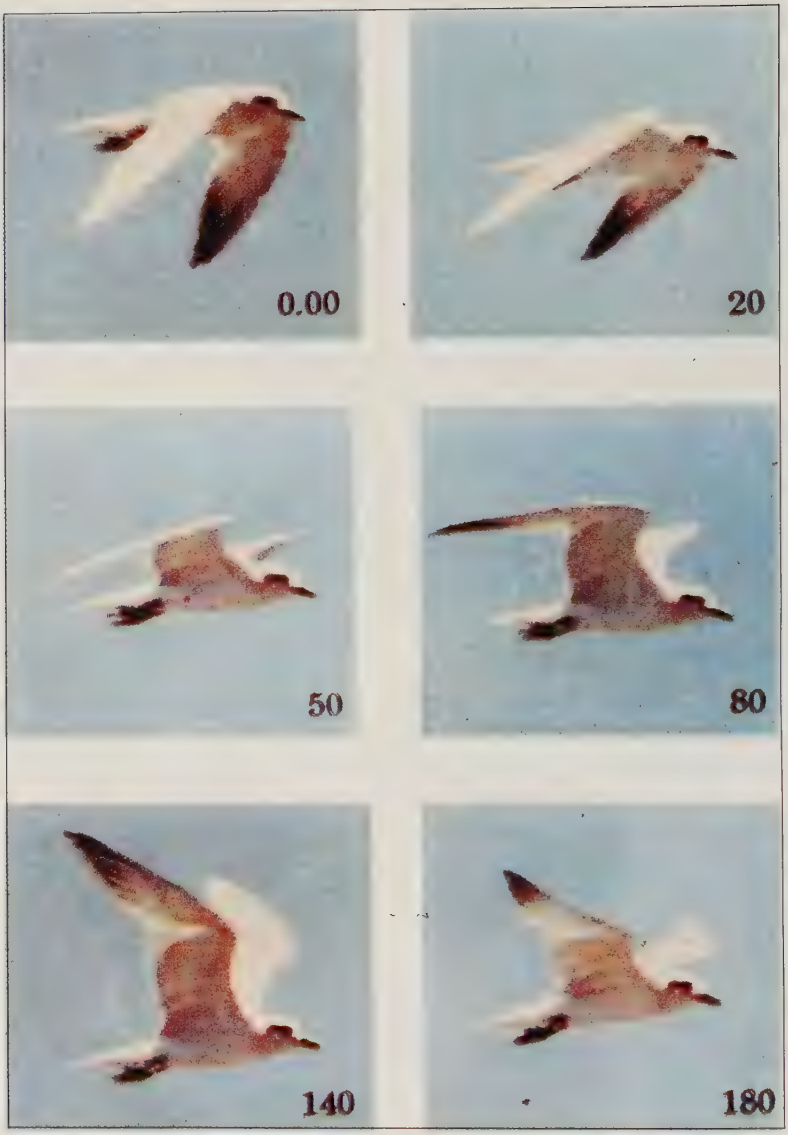


Plate XVII: Tern in flight. Average flapping frequency: 3.5/s. Framing rate: 100/s. Exposure: 500 µs. Lens: f-4.5. The number on the photograph indicates the time in milliseconds.

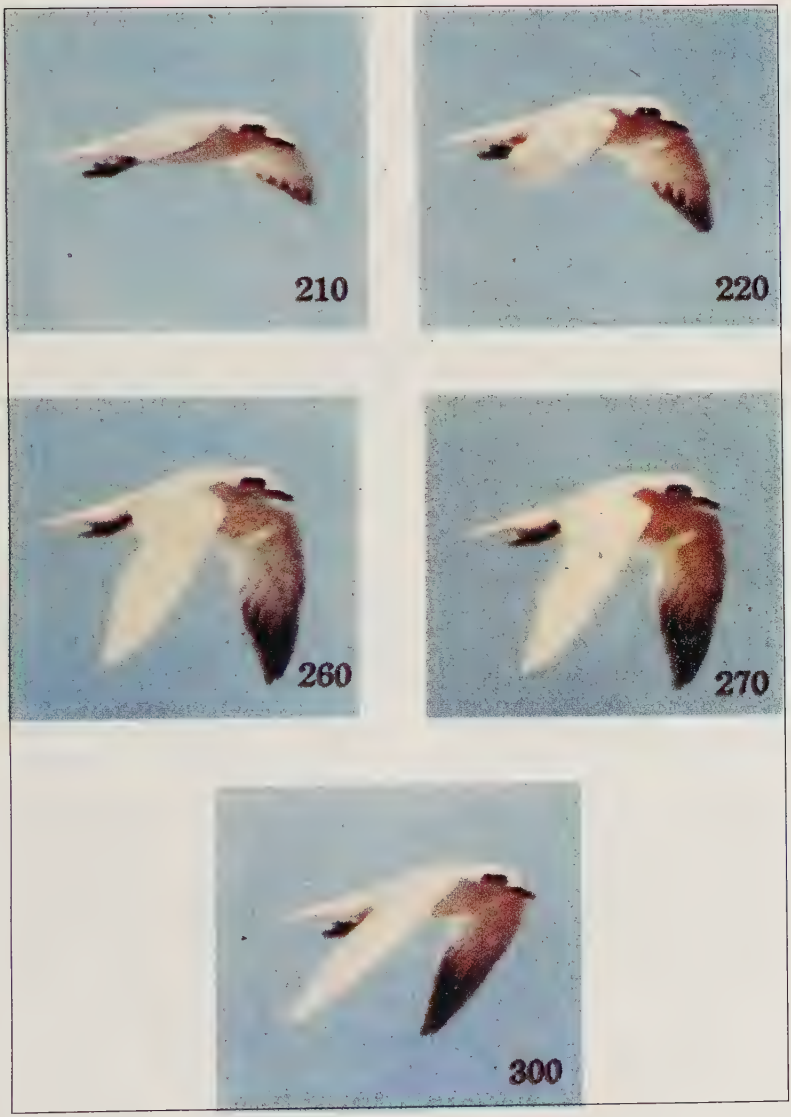


Plate: XVII (*contd.*): Tern in flight.

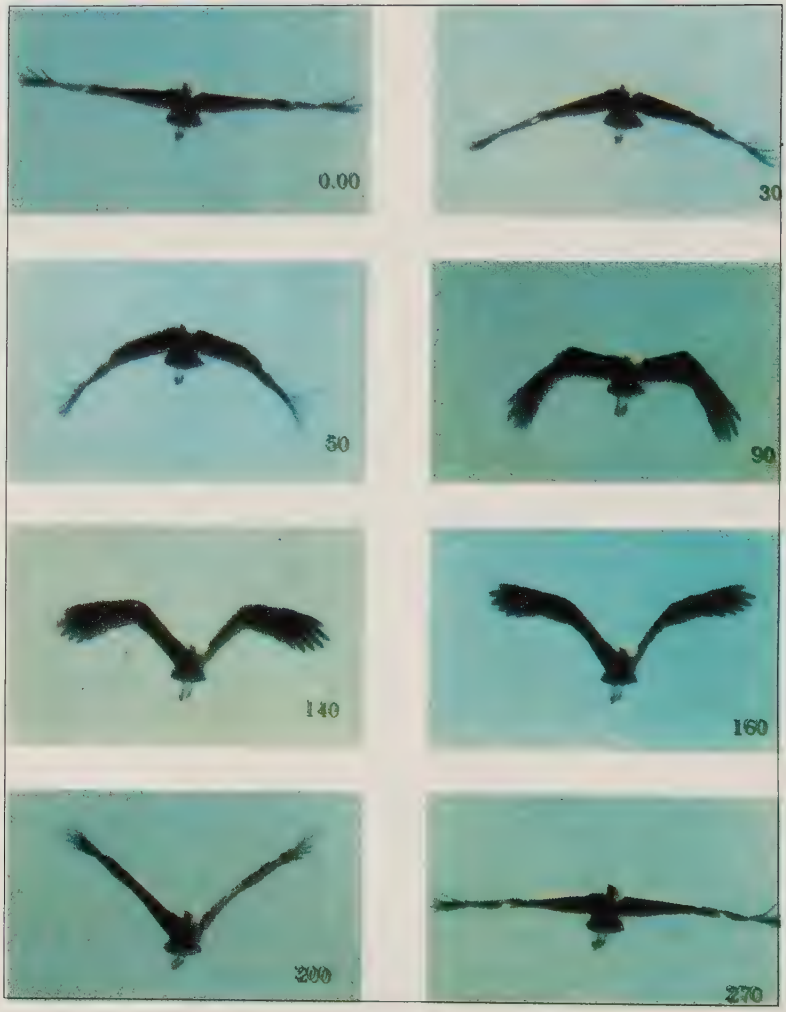


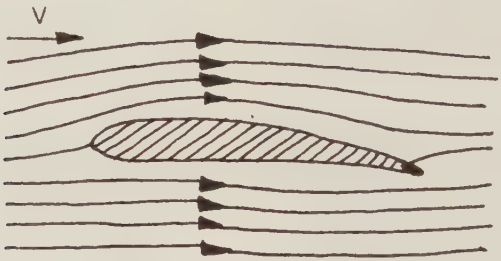
Plate XVIII: Painted stork in flight. Average flapping frequency: 3/s. Framing rate: 100/s. Exposure: 500 µs. Lens: f-4.5. The number on each photograph indicates the time in milliseconds.

that practical airfoils usually have sharp trailing edges). Recall that actual fluids, including air, would stick to the surface, gradually speed up in a thin layer, called the *boundary layer*, and reach the full velocity outside. Due to viscosity, the air next to the surface would have the same velocity as the surface but rapidly fall off as we move away. If, on the other hand, we placed a solid circular cylinder in a rotating circulatory flow, then the velocity would rapidly increase from zero at the surface to a large value at the edge of the boundary layer and then diminish in proportion to the distance.

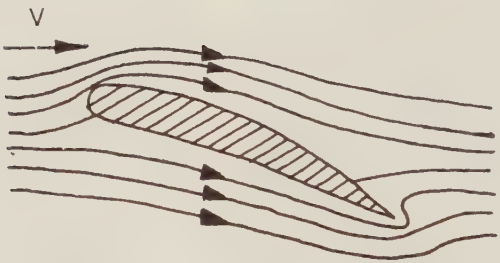
Circulation and Lift

The applications of these ideas to the lift on airplanes and bird wings were pioneered by F.W. Lauchester (England), M.V. Kutta (Germany) and N.E. Joukowski (Russia). According to them, the lift force on the wing is generated by the difference in velocities on the two sides, leading to difference in pressures analogous to the case to the circular cylinder with circulation (Fig. 18). The magnitude of the lift is roughly proportional to the angle of incidence and increases linearly up to a certain maximum value after which it suddenly decreases. This phenomenon, known as stalling, is caused by the viscous boundary layer on the upper surface breaking away; thus, causing a loss of the suction pressures. The flow can be re-attached by re-energising the upper surface layer flow, for instance, by a leading edge slot. The lift can then be increased to higher incidences.

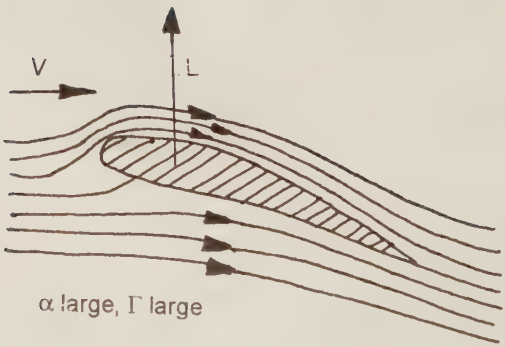
The above discussion can be summed up by the noting that the flow pattern around a wing with an airfoil cross-section generates a velocity field (Fig. 19). The trailing vortex system creates a 'downwash' at the wing which vectorially rotates the free-stream velocity downwards.



α small, Γ = O



α large, Γ = O



α large, Γ large

Fig. 18: Flow past an airfoil.

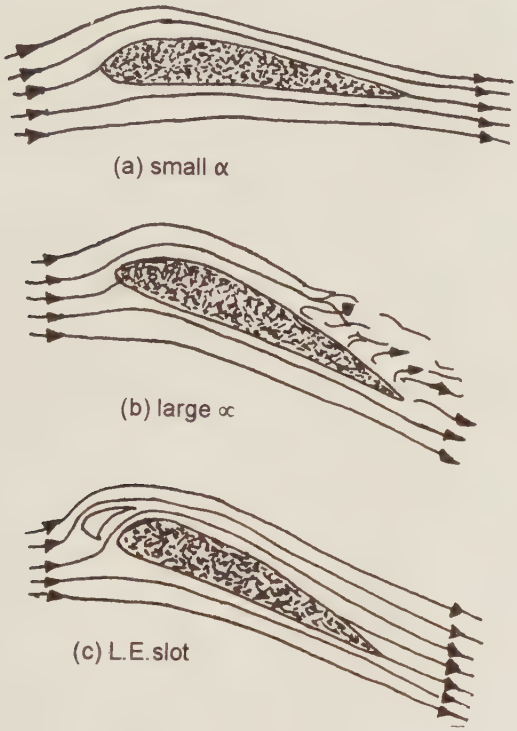


Fig. 19: Lift on an airfoil.

Thus the resultant lift force vector rotates backwards. This gives rise to a force in the direction of the flow, i.e. drag, in addition to lift, the upward force at right angles to the flow direction. In addition to this drag 'induced' by production of lift, we also have the drag caused by viscosity or friction.

So far we have discussed the forces generated by the uniform motion of aerodynamic elements, i.e. airfoils and wings. In the case of birds the requirement for sustained flight requires the generation of both lift and thrust from the

same aerodynamic surfaces, in contrast with flying machines in which the mechanisms of lift and thrust generation are separated. It has been argued that the flapping wing motions required to achieve the necessary forces can be approximately viewed as a linear combination of a simple up-and-down oscillation, with a twist of the wing surface at each extreme of the oscillation *and* a simple constant angle of attack for lift. During the up-and-down strokes the wing surface retains an approximately fixed inclination such that the movement has always a backward facing component which generates thrust. The wing remains approximately inclined at a small angle during the downstroke and then twists into a 'nose-up' position for the upstroke. The air forces producing thrust oppose the wing movements during both the down- as well as upstrokes. On the other hand, in lift production, they oppose the wing's movement downwards but assist it during the upstroke. As a consequence, the wing is heavily loaded during the downstroke and this explains the large size of the main pectoralis muscles responsible for the power stroke, and the much smaller supracoracoideus muscle which acts during the upstroke. Another important aspect relates to the essentially unsteady nature of flapping wing aerodynamics. The complexity of bird flight essentially arises from the non-linear interactive relationships between the wing motions and the aerodynamic and elastic forces.

Flapping Amplitudes and Frequency

In normal horizontal flight the flapping amplitudes are comparatively low — approximately 60° up and down from the horizontal. The frequency of flapping varies with the size of the bird and has been found to vary inversely with size.

To sum up, bird flight can be characterised by flapping and/or gliding. The bird wings are essentially forms of airfoils which, when moving through the air, generate lift and thrust and are subject to drag or resistance. In order to understand the broad features of bird flight in terms of aerodynamic theory, we note that drastic simplifications of the complex wing motions will be called for. In discussing how the bird wings generate enough lift and thrust to move its weight through the air, overcoming the resistance, we will have to make simplifying assumptions which may not be accurate in detail but are physically plausible and lead to results which can be checked and compared with observation.

The basic aerodynamic requirements for sustained flight are:

- Enough lift to balance body weight.
- Enough forward thrust to balance backward body drag.

We have earlier noted that, in contrast to aircraft, the wings of birds have to generate both lift and thrust. As a consequence the bird wing motions, and the forces on them which arise due to interaction with the air, are much more complex to analyse and quantify. The main aim in applying mechanical principles to bird flight is to relate the forces acting during flight to parameters such as wing dimensions and total weight and arrive at estimates of the power required and speed attained. In this process many simplifications of, and approximations to, the observed flight phenomenon become necessary. The estimates and calculations provide information and, sometimes, explanations of wing shape, overall weight or musculature and their relation to the flight habit or habitat. A knowledge of the aerodynamic parameters often allows appreciation of

the difference between types and species of birds.

The amount of life and drag generated by the motion of a wing through the air depend upon five main factors:

- The shape of the wing (cross-section as well as planform).
- Angle between the surface of wing and direction of air stream.
- The area of the wing.
- The density of the air and its kinematic viscosity.
- The velocity of the air stream relative to the wing.

5

POWER FOR FLIGHT

From these factors, components of drag can be estimated, and then it is possible to estimate the power required for steady horizontal flight. The rate of expenditure of energy represents the power to keep the bird in flight. The energy must come from the bird's muscles which in turn derive it from the bio-chemical energy generated by the oxidation of fuel — which may be a carbohydrate or a fat. The mechanical power finally available for flying is only a fraction of the metabolic power, since part of the energy is converted into heat and another fraction used to maintain the basal metabolism for circulation of blood and oxygen in the bird's system. The overall efficiency of energy conversion has been estimated by physiologists to be between 20-25 per cent.

When flying horizontally the life L must equal the weight W and the thrust T must balance the drag D. Since the power P is the rate of doing work we get the following:

$$L = W$$
$$D = T$$
$$P = T.V = D.V$$

where V is the constant horizontal flight velocity.

Apart from normal forward flight many birds also hover, that is, remain at the same place while flying. It must be noted that sustained hovering flight is uncommon

in birds except in the humming bird family. Most birds use the typical horizontal wing motions of hovering for brief periods in transition flight during take-off and landing. The transition between hovering and fast forward flight is much more complex aerodynamically. The birds have to remain airborne during take-off and landing at speeds lower than the stalling speed. The analysis of this speed regime is much more complex and requires combined consideration of the thrust and lift generation modes. Quantitative estimates require a consideration of the wing flapping cycle in greater detail with each wing section from shoulder to wing tip being given consideration. It is found that, due to flapping motions, there is an additional drag penalty to be paid in thrust generation. In conditions of slow forward flight, with large amplitude flapping, the local air speed over the wing sections is significantly enhanced during the downstroke and this results in an 'effective' lift coefficient, significantly larger than the normal forward flight. The increase may be as large as 75 per cent.

Gliding and Soaring

Gliding in still air, in a 'slope current', or rising air can be analysed as a special case of horizontal powered flight with the power being supplied by gravity and the bird with outstretched wings moving in a straight line, inclined downwards. In still air, the plane of flight would be inclined downwards at an angle to the horizontal, the weight W acting vertically downwards. The weight W can be resolved into two components: $W \sin \propto$ along the flight path and $W \cos \propto$ normal to it. For a steady glide the total D must be equal to the driving weight component $W \sin \propto$ and the lift must balance $W \cos \propto$, i.e.

$$D = W \sin \propto$$

$$L = W \cos \propto$$

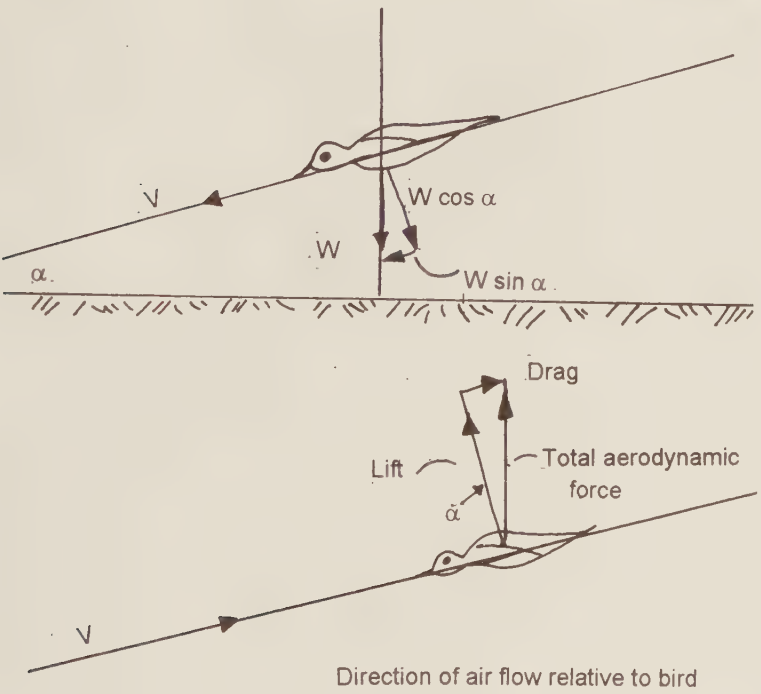


Fig. 20a: Forces on a gliding bird.

Birds with relatively heavier bodies and smaller wings glide faster than those with light bodies and large wings (Fig. 20a). The ultimate in steady gliding occurs when the bird increases its speed by drawing its wings very close together. From a shallow glide the bird then enters a dive — the speed, glide angle and sink, all increase. This manoeuvre taken to an extreme can result in an almost vertical dive. In this configuration the resultant aerodynamic drag at high speed dominates and is almost equal to the weight.

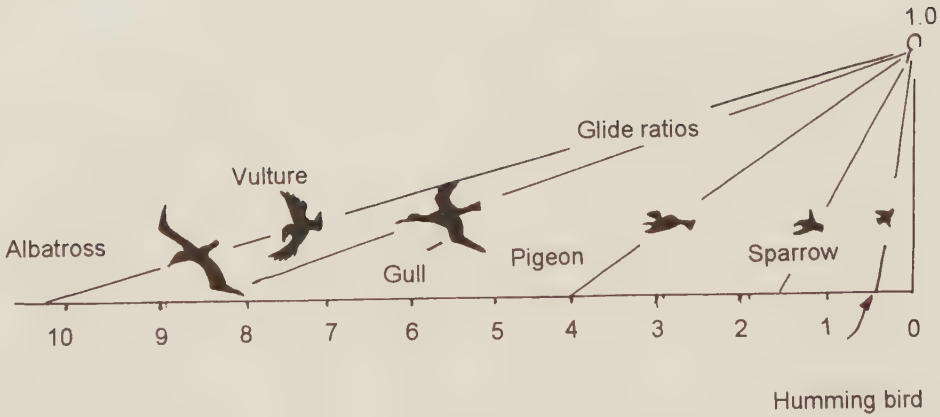


Fig. 20b: Gliding flight.

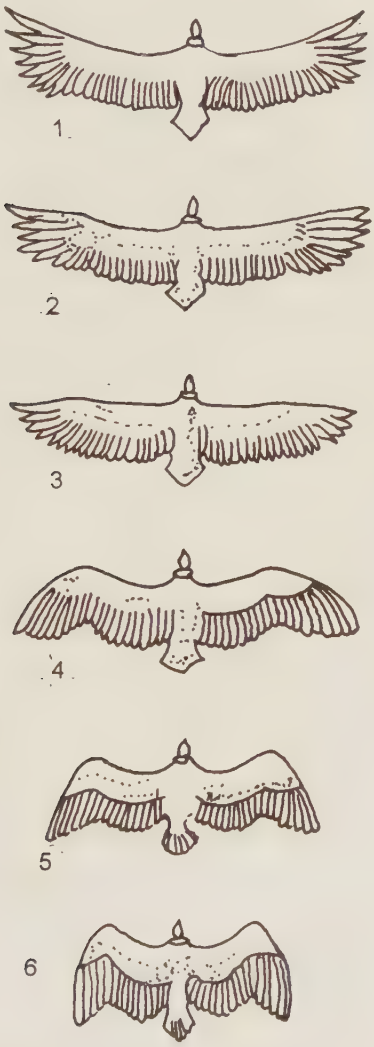


Fig. 21a: Glide speed changes with wing planform. Wing configurations during gliding of vulture (gyps): (1-minimum sink, lowest speed; 2-low speed glide; 3-normal soaring; 4-increased speed; 5-high speed glide; 6-fast dive).

Raptors are typical examples of birds which adopt such aerial manoeuvres. The peregerine falcon kills its prey in the air by striking it from a steep, high speed dive (Fig. 20 b).

Effects of Head and Tail Winds

While for aerodynamic performance the relative motion of a gliding bird is of importance, from a biological viewpoint the motion relative to the earth is of considerable

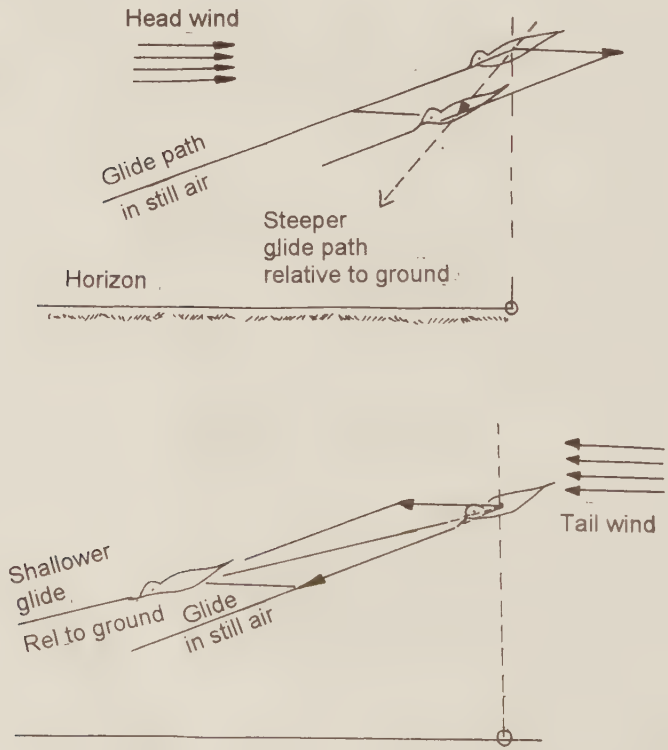


Fig. 21b: Effect of wind on ground speed and glide path.

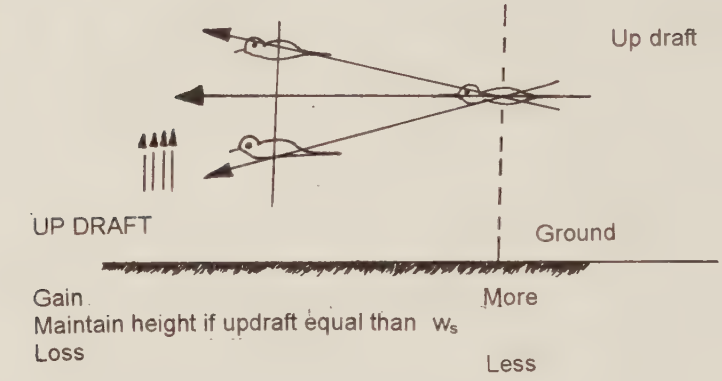
significance. In still air, the air speed and the ground speed are identical but, when the air is in motion, as it is often in the atmosphere, the bird's ground speed is then the vectorial sum of the flight speed and the speed of the air relative to the ground (Fig. 21 a & b).

Soaring Flight

A gliding bird can, without much muscular effort, maintain its height or even increase it if it can derive energy from the air through which it is flying. Clearly a horizontal current of uniform speed cannot provide the necessary energy. However, if the wind has an upward component, or an updraft, then, depending on the magnitude of the upward component, the gliding bird may reduce its angle of glide (Fig. 22). Air streams having upward components of velocity are often found to occur on the windward side of cliffs and mountains. Birds with low wing loading and/or high aspect ratio wings can, with relatively low minimum drag speeds, often exploit these wing conditions. Known as 'slope soaring', the birds which often exploit such conditions are crows, ravens, gulls and various birds of prey.

The substantial vertical components of wind velocity in atmospheric thermals make them ideal for soaring. Thermals occur when disparate heating of the ground takes place. This may be due to vegetation bordering bare or sandy ground or water bodies or even differential cloud cover. Indian cities afford a familiar sight — especially in the mornings — of raptors such as buzzards, vultures, kites and eagles circling aloft for long periods of time

The soaring flight of vultures and other birds usually consists of two phases: circling and gliding. In the circling phase the bird's flight consists of a series of circles or loops with a continuous increase in height. In this phase the



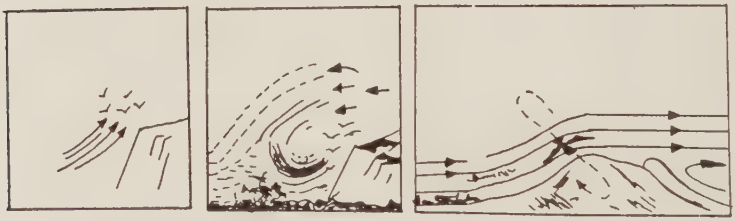


Fig. 22: Soaring flight. The figure shows how a gliding bird may maintain its height or even increase it.

wings are fully extended and the tips of the primary feathers spread wide. As the bird moves in the circular path its wings are banked towards the centre of the circle and a centripetal force comes into play so that the turn occurs without side slip. Gaining height, the bird partially flexes its wings; it may remain circling, but no longer gaining height. This configuration would be adopted in searching for food, etc. On the other hand, after reaching a certain height, the bird may flex its wings into a fast glide configuration and glide along a straight path, losing height as it glides. After some time, and at a variable height above the ground, the bird may again adopt the soaring configuration, fully extending its wing, and resume circling and gaining height. E.H. Hankin has described in detail the soaring flight of Indian birds in Agra. He found that soaring began at a definite period of the day and was closely correlated to the intensity of sunshine. The time of soaring depends on the wing loading of the birds. The first to appear were the *cheels* (*Milvus govinda*) with a wing loading (weight/wing area) of approximately 0.27 gm/cm^2. About half an hour later came the scavenger vultures (*Nephron gingianus*) with wing loading of 0.42 gm/cm^2. White-backed vultures (*Pseudogyps calvus*) with wing loading of 0.55 gm/cm^2 followed another half an hour later. Then appeared the black vultures (*Otogyps calvus*) with wing loading of 0.6 gm/cm^2 about an hour and a half after the *cheels* began. In general the circling diameters of the circle increase with the wing loading. *Cheels* circle in about 15 metre diameter circles while the heavily-laden vultures have circles of the order of 50 metres.

Dynamic Soaring

In contrast to land birds such as vultures, oceanic birds, notably petrels and albatrosses (*Diamedeidae*), usually

restrict their gliding flight to relatively low altitudes. They have evolved a special soaring technique known as 'dynamic soaring' which involves flight within the shear layers of air just above the surface of the sea. Close to the sea surface the wind increases to appreciable speeds at higher altitudes. In fact, the wind profile approximates a typical shear or boundary layer and the ability of the albatross to soar in this approximately 10-15 metre layer of wind does not depend upon vertical air components, but on an entirely different mechanism for extracting energy from the wind. It is interesting to note that the explanation of this mechanism of energy extraction from a shear layer was first given by Lord Rayleigh in 1883.

During the first phase the bird glides directly into the wind, gaining height but losing ground speed as a result of the combined effects of gravity and drag. Near the peak of its climb the bird executes a 180° turn and faces downwind to start the second phase of its flight. During this high-speed glide the bird loses height and rapidly increases its ground speed, thus increasing its kinetic energy at the expense of the potential energy (height loss). Approximately close to the sea surface the bird again executes a 180° turn and repeats the first phase. The reason that the albatross is able to repeat its flight pattern indefinitely is because during the long downwind glide it is able to extract sufficient energy from the wind to counteract the energy being dissipated in overcoming drag. The explanation lies in the extra inertial force term in the energy balance for the motion which is given by minus mass times acceleration (Fig. 23).

Typically the albatross' air speed is about 30 metre/sec (100 km/hr) and with g=9.81 m/sec^2, the gradient of wind has to exceed 1/3 metres/sec per metre. This is usually available in the lowest 10-15 metres of the air above open

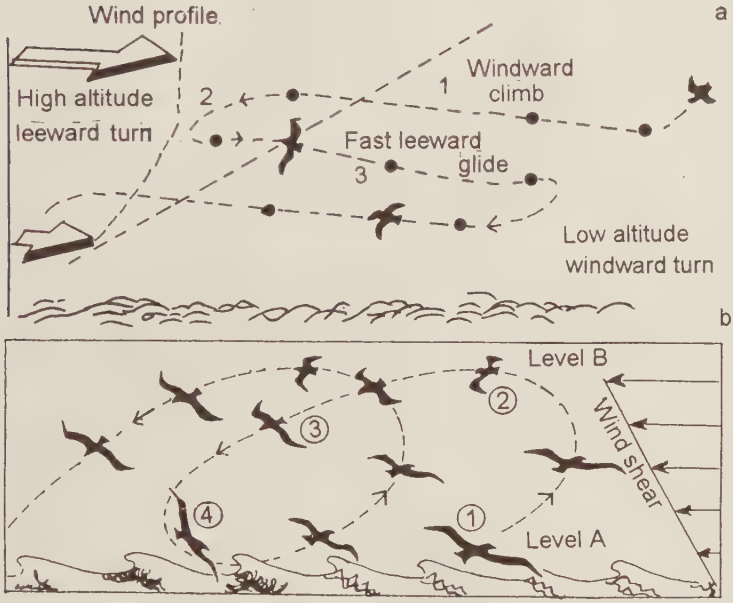


Fig. 23: Theory of dynamic soaring. (a) Phases in the soaring flight of an albatross; (b) dynamic soaring: (1) rise into wind; (2) turn at highest point; (3) glide downwind build-up of speed; (4) turn and repeat.

sea. For higher gradients the bird's air speed can be less. It is interesting to note the analogy between the albatross' dynamic soaring and the energy balance governing turbulent shear flows in fluid mechanics. The condition for the large eddies extracting energy from the mean flow turns out to be similar to that for the bird.

6

POWER AVAILABLE

The mechanical energy for flight (in general, animal locomotion) is derived from chemical energy which comes from the oxidation of suitable fuel (usually fat and carbohydrates). It is usual to measure the rate of metabolism as the rate of consumption of oxygen. One litre of oxygen consumed corresponds to 20 kilo joules or 4.8 kilo calories. In the more usual units, 1 litre per hour oxygen consumption represents 5.6. watts power output. In the absence of external activity, the rate of metabolism can be called the 'resting', or 'maintenance' or 'basal' metabolic rate. In warm-blooded animals, mammals and birds, this basal metabolic rate is relatively well defined and the body temperature of the animal remains relatively constant. The maintenance metabolic rate in watts and body mass (in kilograms) are correlated by the well-known 'mouse to elephant' curve.

Although a wealth of information is available about the maintenance metabolic rates of animals and birds, our knowledge of maximum continuous performance or peak power output remains very meagre (Fig. 24). It is known that in some animals the peak power output during maximum exertion may exceed the maintenance level by a factor of 10 or 15, or even 20. Power output of birds in flight has been reported to exceed their basal rate by a constant factor of about 10, independent of body size.

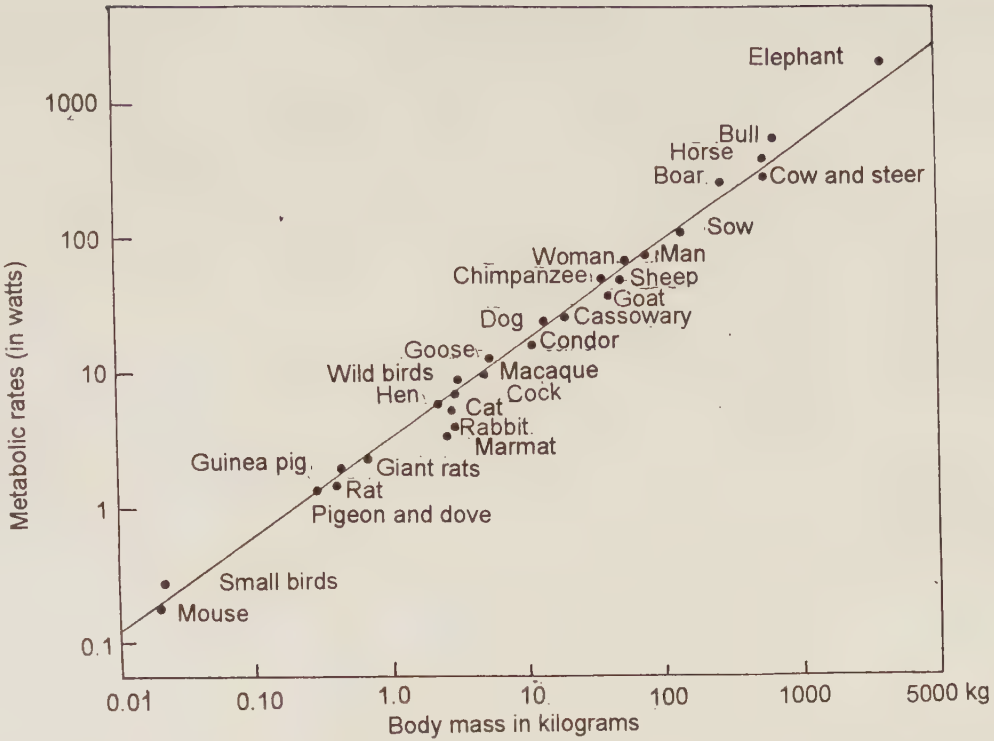


Fig. 24: Metabolic rate and mass in animals.

However, the available information is insufficient to conclude with any degree of certainty that this factor is really scale independent. In fact, it is known that peak power output in small birds can be very high (e.g. humming birds) while in larger birds, like vultures, it is not so large.

Muscle Power

Extensive data for birds compiled by C.H. Greenewalt indicates that the main flight muscle of birds, the pectoralis, makes up for about 15-17 per cent of the body mass. Obviously there are variations in this figure related to the flight muscle of individual species, but the percentage is a fairly constant fraction. The supercoracoidus (elevator) muscle weight is usually about 10 per cent of the pectoralis. We have noted earlier the exceptional capabilities of humming birds and it is therefore not surprising that their flight muscles make up a larger fraction of the body mass, some 25-30 per cent. Also, in these birds, the secondary muscle responsible for the wing upstroke makes up about 30 per cent of the total mass of the flight muscles compared to only about 10 per cent in other birds. This suggests that lift is generated in both the strokes during hovering and, of course, is in agreement with the analysis of wing movements of hovering humming birds.

The maximum tension per unit area or stress that a muscle tissue can generate is roughly 3-4kg/cm^2. This maximum stress is known to be independent of body size. Thus, if the work per contraction is constant, the power output during contraction will be a direct function of the speed of shortening, i.e. the strain rate. For repeated contractions, as in flight, the average power output of a muscle will be directly proportional to the frequency of contraction.

Fuel and Oxygen

For steady state power output, the muscle must receive a continuous supply of fuel and oxygen at the appropriate rate. The bird's respiratory system is designed for high demands. The paired legs are connected to five pairs of air sacs branching throughout the body — even to the bones. Bird lungs have two-way flow of oxygen. If the muscles get overworked it can lead to an oxygen crisis. To prevent such an emergency, birds, which must make a prolonged flight effort, have a built-in oxygen reserve. Two typical kinds of flight activity are: prolonged cruise, for example, during migration, and sprint when, for example, escape from a predator is called for and a sudden burst of power is required. The muscular structure caters for such requirements through built-in oxygen reserves or by allowing anaerobic oxidation to take place for short periods. The muscles used in locomotion are composed basically of filaments of two types:

- Base protein myosin filaments, which are thick.
- Base protein actin filaments, which are thin.

The supply of energy essentially is derived from oxidation of fuel which takes the form of fats and carbohydrates. The energy yield from oxidation of fat is nearly twice that from the same weight of carbohydrates. Also, carbohydrates need to be stored in hydrated form. So, for a given amount of energy, the mass of fuel to be lifted is about eight times more for carbohydrates than for fat. For long flights maximum energy is required from the least weight of fuel. This fat is the most suitable form of fuel. However, fat can be used only by aerobic oxidation in the muscle fibres themselves and cannot incur oxygen debt. Thus in prolonged flapping flight, the muscles must operate under quasi-steady state conditions with the right

amount of blood supply, etc. It therefore turns out that such muscles for the 'long haul' are rich in mitochondria and also contain myoglobin. These components give to the muscle a red colour. Muscles used for sprints of short period generally contain glycogen which is oxidised anaerobically at the expense of running up an oxygen debt. Such muscles are white in colour and generally larger in diameter than the red cruise muscles. Some birds (e.g. pigeons, terns, crows) have fibres of both types intermingled in the pectoralis muscles. The bird can then use the appropriate ones (red) for cruise and call forth the white ones for peak exertion during peak effort, e.g. at take-off or escape from attack by a predator. The game birds (*Galliformes*) are typical birds which fly only briefly; they have preponderance of white fibres in their flight muscles. However, in most birds which need to fly continuously for periods of time, red fibres predominate. To summarise, fat is the more efficient fuel for steady, long period flight and carbohydrate, which can be more quickly mobilised, is the fuel used for sprint or emergency power. In general, of the total metabolic energy produced, approximately 20-30 per cent appears as mechancial work, the rest being dissipated as heat.

Structure and Action of Muscles

Physiologists have established that broadly the structure and action of muscles in all vertebrates is more or less similar. Functionally, most muscles require more or less regular cycles of contraction and relaxation. Muscle fibres contain contractile material called 'myofibrils', approximately 1μm in diameter. As noted earlier, muscle contraction occurs due to interaction of two kinds of protein filaments:

- Thick filaments composed mainly of myosin.

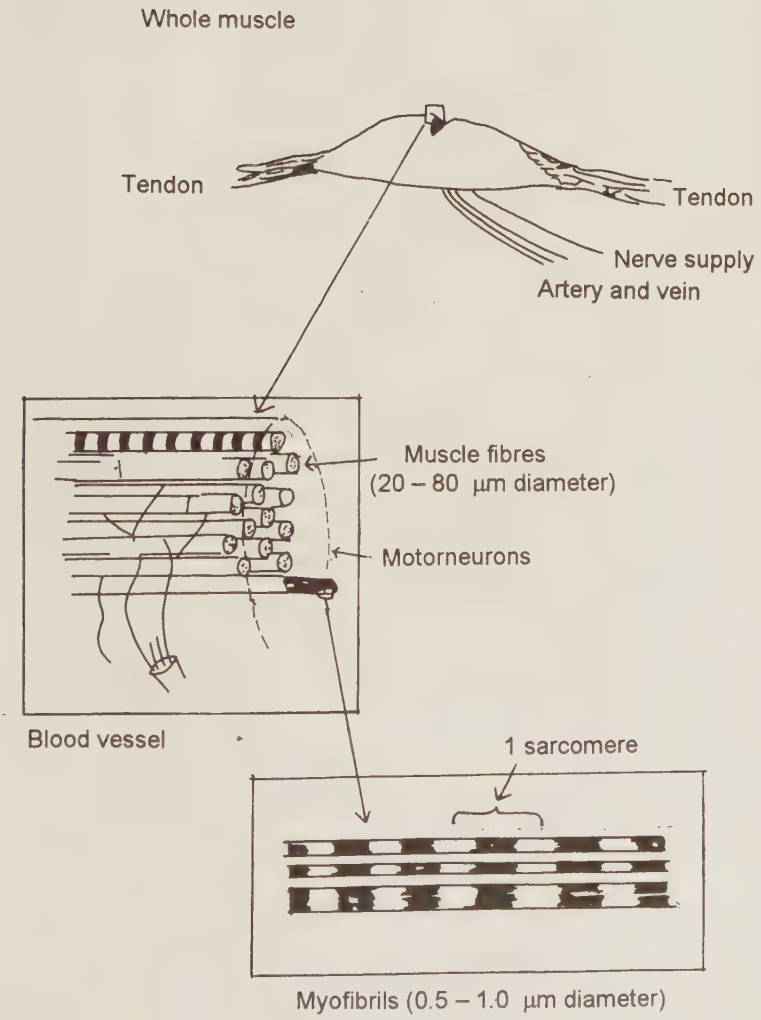


Fig. 25: Structure of muscles.

- Thin filaments containing actin.

The thick and thin filaments are arranged in a regular pattern which appears as bands when observed under the microscope. Each unit of the repeating pattern is called a 'sacromere', which is the basic unit repeated along the length of the muscle. Each sacromere consists of one set of thick filaments and two sets of thin filaments which overlap with the thick ones. The thick filaments have protruding cross bridges which, when activated, interact with the thin filaments and generate a force (Fig. 25). The force per unit cross-sectional area that a muscle can generate depends upon the number of filaments in parallel. It is found that the filaments and myofibril packing is about the same in most species. Therefore this is scale-independent. When muscles exert a constant force while shortening, it is called *isotonic contraction*. When muscle fibres develop force (tension) without an appreciable change in their length, it is referred to as *isometric contraction*.

The power output of a muscle is limited by the rate at which its metabolic processes can produce ATP (adenosine triphosphate) and the rate at which its myofibrils can transduce the chemical energy into mechanical work. The metabolic and mechanical processes occur in separate fractions of the volume of the muscle: myofibrils transduce chemical energy to mechanical work; mitochondria is responsible for the production of ATP.

Bird Flight

In the case of birds, *flapping flight* involves *isotonic* contractions of roughly constant velocity and *gliding flight* involves mainly *isometric* contractions.

During flapping flight the bird can, in principle, alter its speed in several ways. However, it is found that in

general it does not, to any appreciable extent, change the rate at which the pectoral muscle fibres contract, so the wing beat frequency remains roughly constant. Thus, the bird changes the shape and force of the stroke. It turns out that there is an optimum rate of shortening of the muscle fibres at which maximum power is produced. This implies that for each kind of bird there is a definite frequency of wing beat. We have seen this earlier also.

Wing Frequency

Flapping frequency varies considerably between different species. Large birds, like the stork or pelican, flap at about 2 beats/sec while for small birds, like a wren, the wing frequency is around 10 hertz. Other medium size birds have flapping frequencies in between. Large birds do not need to flap their wings as fast as small birds in order to achieve the necessary power for flight. Power being force times displacement over time (velocity), the greater wing span of the larger birds means increased displacements. The time of displacement may also be increased. So they can have a longer beat cycle (lower frequency). It also turns out that there are limits to the wing beat frequency for large birds. The muscle fibres in large birds are long with a lot of sacromeres and if they had the same intrinsic speed of shortening, they would develop very high strain rates which the material, of which muscle fibre is made, cannot withstand.

The muscles involved in gliding are primarily those which hold the wings forward and outstretched, and the pectorals which maintain their horizontal position. The energy needed for gliding is known to be considerably less than that needed for flapping flight. The metabolic rate during gliding flight of herring gulls is only about twice the resting metabolic rate, while in flapping flight it may be

about seven times. Roughly speaking, these proportions seem to hold for most birds (the exception are humming birds which can continuously hover and can put out extraordinary amounts of power).

Power Output from Muscles

The total power that a bird can put out over and above the part required for maintaining the basal metabolism and circulation of blood and air can be called the 'power available'. Actually for flight, the conversion efficiency to mechanical power (or energy rate is only 20-25 per cent of the chemical power produced). Compared to other animals, birds have a significantly higher metabolic rate and higher oxygen consumption. While most mammals have hearts which are about 0.5 per cent of their body weight, in birds it is about 1 per cent.

The maximum power output from a muscle occurs when the muscles are contracting at their optimum speed and developing the optimal stress. Contracting muscles can develop stress of 200-400 kN/m^2 but the maximum power occurs when they shorten against one-third of the maximum stress, i.e. against 70-130 kN/m^2. In this condition, the strain rate (shortening speed) is about 20 per cent of the maximum value. It has been found empirically that the maximum work done per contraction, when calculated per unit volume, is invariable and independent of size. The power output is a direct function of the strain rate and, for repeated contractions, the average power output of a muscle is directly proportional to the frequency of contraction. The frequency varies with bird size. Typically large birds have low flapping rates around 2 hertz and small ones, about 10 hertz. It has been found that the average continuous power developed is about 70-260 watts per kg of muscle (specific power) and the specific

power of birds is in the range 50-200 watts/kg.

The specific power in watts per gm of mass of bird varies from 0.054 for the vulture to 0.235 for the humming bird. The vulture can sustain this power output only for short periods while the humming bird can sustain a much higher output continuously for long periods. Perhaps the most detailed data available is for the pigeon (*Columba livia*) which has been studied in detail.

7

EFFECTS OF SIZE AND SHAPE

During the evolutionary processes three kinds of morphological changes have taken place in birds:

- The wings of birds have lengthened. The area swept during flapping has increased, thus lowering the induced power to manageable levels at low speeds.
- The muscular system has got modified in such a way as to transmit large amounts of power to the wings.
- The body has become streamlined for drag reduction.

The above general observations need to be modified and supplemented when considering a particular species or order of bird. Here the evolutionary processes are intermingled with the environmental and ecologist factors.

Bird flight has two major areas of complexity. The first derives from the fact that flight provides the bird an extended range of means for its life and development. Some of these are escape from predators and other dangers; seeking, finding and talking food; migration; and for reproductive purposes. Many different modes of flight are used. These include straight and level flight, climbing, diving, bounding, soaring, take-off and landing, hovering and manoeuvres such as zig-zagging, etc. The other area of complexity arises from the highly non-linear interaction between a bird's flight activities which generate lift for weight support and propulsion for overcoming drag. The

problem of scaling and explaining the effects of departures from geometrical similarity is indeed a very difficult and complex task. There are complex connections between the scaling of biological form and function and various aspects of geometrical, mechancial, physiological similitude. In particular, the unique bird organ represented by the wing shows variations in shape, form, size and weight which are difficult to correlate in detail with physiological and biological parameters dictated by the lifestyle of bird species.

Scaling Laws

By considering the changes in size while maintaining generally the shape one can discuss changes in flight behaviour and characteristics of flight of birds in a rational manner. Of course, dimensional analysis is strictly applicable only for cases of geometrical similarity. However, even when this does not hold precisely one can derive useful information.

We begin by noting that bird size may be expressed in terms of wing span, body weight, wing area, etc. The main parameters which enter into discussion of bird flight are broadly the flight speeds and the power required and power available for a particular regime of flight. We note that the 'size' of a bird generally implies the weight as well as the dimensions of wings and body, etc. A bird's weight is proportional to volume, which has the dimensions of l^3 where l is characteristic length or dimension. The wing area is proportional to l^2. Thus we note that the wing loading, which controls the flight speed, is proportional to l.

Since velocity is proportional to the square root of the wing loading, we note that flight speed V would vary as $l^{1/2}$. The minimum power required for sustained flight is given by the product of the drag and velocity and evaluated at the minimum power speed. For an estimate of the

power available, there is an upper limit to sustained rate of working of the muscles.

We can now assess and compare the flight behaviour and requirements of birds of different sizes. A bird *A* with twice the wing span of a bird *B* would fly $\sqrt{2} = 1.4$ times as fast. In terms of weight, since $l \propto W^{\frac{1}{3}}$, the heavier bird would require $(2)^{\frac{7}{6}} = 2.25$ times the power to fly. On the other hand, the heavier bird will have only $(2)^{\frac{2}{3}} = 1.59$ the power available. Thus, in relative terms, the larger and heavier birds can be expected to have reduced capabilities of climbing flight by flapping — a point we have noticed already. This proportionate decrease in power margin with increase in size, suggests a limit to the size of birds that can fly.

Such scaling arguments cannot, of course, provide the actual numerical estimate for the maximum practical limit for flying birds but they do indicate the existence of an upper limit which has to be determined from observation (Fig. 26). From observational data it would appear that four orders of birds given below generally conform to the scaling laws for a limiting weight for flying. This turns out to be about 12 kg.

- Kori bustard (*Gruiformes*).
- White pelican (*Pelicaniformes*).
- Mute swan (*Anseriformes*).
- California condor (*Falconiformes*).

The first proportionality, relating the wing loading and weight, is a well-known relationship. Extensive data on birds are available showing dimensional relationships and confirming the scaling laws discussed above. One can, of course, expect departures from the one-third power law as well as those governing the characteristic velocities and power relations. It is not surprising that small birds, like

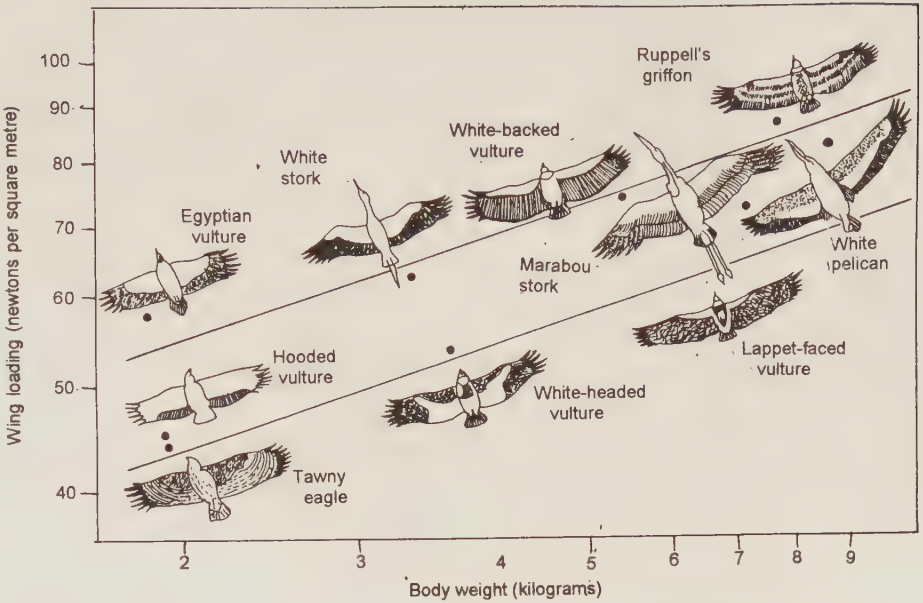


Fig. 26: Wing loading and size of soaring birds.

the partridge or the humming bird, significantly depart from the mean behaviour indicated by the scaling laws.

C.H. Greenewalt's extensive studies show that a large number of groups of birds very roughly conform to the scaling laws. These include: falcons, ducks, coots, divers, herons, woodpeckers, wrens, grebes, pigeons, swans, owls, etc.

Wing Shape

The wing is the bird's unique possession and totally committed to flight. Adaptation of the wing to the bird's requirement for food and preservation in different habitat and its mode of life, has produced a very large variety of wing shapes and forms (Fig. 27). However, avian morphologists distinguish four basic wing types with many intermediate forms:

- *The elliptical wing:* The shape is relatively short and broad with a low aspect ratio between 3 and 6. Wing loading is moderate or low. The wing beat is fairly fast and the amplitude moderately large. This shape typifies many game birds, woodpeckers, cuckoos, jays, etc. (many *Passeriformes* and some *Galliformes* and *Columbidae*), i.e. birds which have to manoeuvre through restricted openings in vegetation. The alula is relatively large and the primary feathers may separate to form additional wing slots to prevent stalling at low speeds.
- *The broad soaring wing:* This occurs in vultures, eagles, pelicans, etc. The shape is moderately long and broad with aspect ratios between 5 and 7 and only moderate wing loading. The beat frequency is low. The alula and wing slots are prominent. This type of wing is particularly suited for low speed soaring.
- *The high speed wing:* This characterises swifts (*Apodidae*), falcons (*Falconidae*), humming birds (*Trochilidae*)

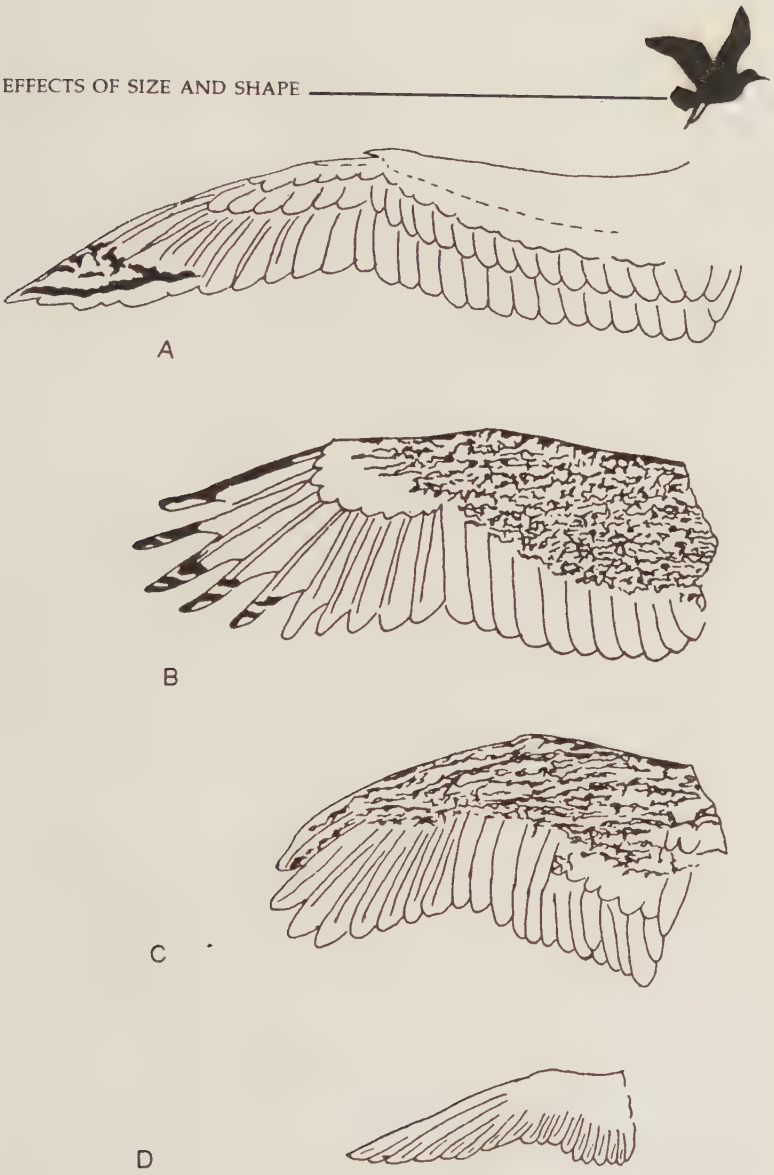


Fig. 27: The four basic wing shapes: (A) long distance high speed gliders: albatrosses, gulls, shear-waters and other sea birds; (B) endurance land soarers: eagles, vultures, storks, etc.; (C) fast flapping rapid take-off game birds and woodpeckers, jays etc.; (D) high speed fliers: swifts, falcons, waders, etc.

and, to a lesser extent, ducks (*Anas*) and terns (*Sterns*). The wing is relatively small with a moderately high aspect ratio between 5 and 9. Drag is low and the wing loading high. The wing beat is rapid and the amplitude relatively small. The wing is tapered and the outer part may be swept back. There are no tip slots except in falcons who close them during fast flight.

- *The long soaring wing:* This is confined to oceanic soaring species such as gulls (*Larus*), gannets (*Mortus bassanus*) and albatrosses (*Diomedeidae*). Long, slender and pointed, this type of wing has a high aspect ratio of between 8 and 18 and high wing loading. With high L/D these birds soar at high speed. There are no tip slots but the alula can be fairly large. Such wings have high aerodynamic efficiency and satisfactorily meet the contradictory requirements of gliding and flapping flight. However, they are relatively fragile and demand a habitat free from obstacles.

The detailed mechanics of the wing vary with different types of flight as discussed before. In fast level flight the propulsion comes almost solely from the downstroke, being provided by the outer half of the wing. During the upstroke the wing is lifted by air pressure and is more or less passive. Considerable lift is generated by the inner part of the wing on both up and downstrokes. The slow flight of small woodland birds while ascending or descending is not very complicated. The main lift and propulsion come from the downstroke. The steep ascending and descending flight of strong fliers of medium size, such as pigeons, ducks, hawks and pheasant is much more complex. The downstroke provides much lift but little propulsion. The upstroke is distinguished by a very rapid

rotation at the shoulder and extension of the arm, producing a backward flick of the primaries which results in strong propulsive forces. In hovering flight, as in the flight of humming birds, much lift is obtained during the forward as well as backstroke. Each species has some peculiarities in its flight, and in the flight apparatus and the mode of using it, but the basic features are roughly similar.

8

CONCLUSION

Flight in the atmosphere imposes limitations and restrictions on the shape, size and structure of flying animals as well as flying machines. If an animal like a bird has to fly, aerodynamic efficiency and power have to be combined with structural strength and muscular energy and the weight must be kept at a minimum. Such requirements have imposed a certain degree of uniformity of basic structure in all birds. Every part of the bird's anatomy is attuned for its life in the air. A compact streamlined body combines strength with lightness and a versatile musculature controlling the unique feather-covered wings provides the bird with an unequalled system for flight.

Over the 150 million years of evolution the anatomy and physiology of birds have changed not only to combine strength and lightness but also to enhance efficiency of body functions, such as breathing and blood circulation. The senses have been very finely tuned to the flight environment. Like all vertebrates, birds sense their attitude changes by means of the semi-circular canal of the inner ear and their marvellous flight control systems depend on this information. Their eyesight provides them with the maximum possible amount of information at the fastest speed reaching a perfection not found in any other animal.

Second only to insects, the birds are the most

biologically successful group of animals that have existed. This success, in which the ability to fly has played a vital part, has led to an extraordinary diversification into nearly 9,000 species compared to about 4,000 species of mammals. Birds cover virtually all regions of the earth, from the polar to the equator. In their quest for food and survival each species has evolved characteristic forms of flight which, while conforming generally to broadly similar features, have specific attributes peculiar to it. Smaller birds have adapted their flying to escape threat. Apart from being highly manoeuvrable, some of them adopt assembly and flight in flocks, e.g. starlings. Another technique is the capability for very high speed spurts for a short time in order to escape. Pheasants and partridges have an almost rocket propelled take-off and fast curving flight for short distances before finding a shrub shelter. Often the special modifications of flight which adapt a bird species to one habitat prevent their switching to another. However, some birds are equally adept in several bio-habitats. Gulls fly over stormy seas as well as the reed masses of inland lakes. Pigeons and crows seem to survive in forests as well as in the concrete jungle of urban surroundings.

The song birds are particularly successful survivors because of their great manoeuvrability in flight. Natural forests, bushes and shrubs covered plains provide ample food supply but are full of obstructions which small birds can easily navigate through — and also find nesting and hiding places in! Despite their lack of endurance some small birds have to migrate before winter and frost. Arctic terns, golden plovers, snipe, geese and many shore birds migrate over long distances in quest for food. Each species has interesting and intriguing features of flight.

Much empirical data is needed to relate the flight

characteristics of a particular bird species to its habitat and environment and habits. There is great scope for naturalists and scientists to pursue these studies in India.

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Appendix

Table 1
Morphology and Lift Data

Birds	*Flight body mass (kg)*	*Wing muscle mass (g)*	*Wing area (cm^2)*	*Wing span (cm)*	*Maximum lift force ($Nx10^2$)*
House sparrow *(Passer domesticus)*	0.033	7.1	80	21	49.2
Pigeon *(Columba livia)*	0.267	59.0	486	57	372.9
Lance tailed mankin (*Chiroxiphia lanccolate)*	0.017	4.4	99	23	29.9
Dark backed goldfinch *(Spinus psaltria)*	0.011	2.3	32	15	15.8
Rufous tailed humming *(Amazilia tzarcatl)*	0.006	1.8	17	12	10.5
Red crowned woodpecker *(Melanerpes rubricapillus)*	0.045	11.4	112	24	60.1
Tropical mocking bird *(Mimum gilvus)*	0.071	13.9	197	31	103.9
Clay coloured robin *(Turdus grayi)*	0.067	19.9	221	36	106.8
Blue-grey tanger *(Thraupis episcopus)*	0.029	8.4	108	23	47.6

Ref: J.H. Marsden: *Jo. Exp. Biol.*, 1987, 130:253.

Table 2
High Altitude Flight of Birds

Birds	*Approximate altitude*
Richard's pipt *(Anthus novaeseelandiae)*	6,100 m (20,000 ft)
Black redstart *(Phoenicurus ochruros)*	6,100 m (20,000 ft)
Blue hill pigeon *(Columba rupestris)*	6,400 m (21,000 ft)
Jungle crow *(Corvus corax)*	6,400 m (21,000 ft)
Raven *(Corvus corax)*	6,400 m (21,000 ft)
Hoopoe *(Upupa epops)*	6,400 m (21,000 ft)
Alpine accentor *(Prunella collaris)*	6,400 m (21,000 ft)
Bearded vulture or lammergeyer *(Gypaetus barbatus)*	7,300 m (24,000 ft)
Alpline chough *(Pyrrhocorax graculus)*	8,200 m (27,000 ft)

Ref: Ward-Smith, A. J.: *Biophysical Aerodynamics and the Environment,* 1984, Wiley Interscience.

Table 3

Vibration in Wing Beat Frequency in Selected Species

Species	*Wing beats per second*
Great crested grebe *(Podiceps cristatus)*	6.3
Cormorant *(Phalacrocorax carbo)*	3.9
Pheasant *(Phasianus colchicus)*	9.0
Coot *(Fulica atra)*	5.8
Peregrine *(Falco perigrinus)*	4.3
Ringed plover *(Charadrius hiaticula)*	5.3
Puffin *(Fratercula arctica)*	5.7
Herring gull *(Larus argentatus)*	2.8
Wood pigeon *(Columba palumbus)*	4.0
Blackbird *(Turdus merula)*	5.6
Starling *(Sturnus vulgaris)*	5.1
Magpie *(Pica pica)*	3.0
Rook *(Corvus frugilegus)*	2.3
Humming bird *(Various spp. hovering)*	22-79*
Rufus humming bird *(Selasphorus rufus)*	200*
Blue tit *(Parus caeruleus)*	25**

* Alexander Skutch, 1974: *The Life of the Humming Bird.*

** Personal recording of slow motion photography.

Ref: Freethy R.O.N.: *How Birds Work,* 1982, p. 88, Blanford Press, U.K.; Blake, Auk, 1974, 64:619-620; Meinertzhagen, Ibid, 1955, 97:11-114.

Laser typeset at Icon Printographics, B-107 Fateh Nagar, New Delhi-110018 and printed at Jay Kay Offset Printers, 17 DSIDC, Rohtak Road, Delhi-110041.

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